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MELBOURNE

THE STATISTICAL ANALYSIS OF THE CANADIAN LYNX CYCLE

I. STRUCTURE AND PREDICTION

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Summary

Trapping records of the Canadian lynx show a strongly marked 10-year cycle. The logarithms of the numbers trapped are analysed as if they were a random process of autoregressive type. Such a process appears to fit the data reasonably well. The significance of this for the explanation and prediction of the cycle is discussed. The results will be used in a later paper to consider how far meteorological phenomena influence the lynx population and may be responsible for the observed synchronization of the cycle over the whole of Canada.

I. INTRODUCTION

The 10-year cycle in lynx and other animals in North America has been discussed by many authors (for references see Elton and Nicholson 1942; Rowan 1950). Trapping records from the Hudson Bay Company over a long period of years are given in Elton and Nicholson's paper. These records show clear evidence of cyclic behaviour. In the present paper it is proposed to analyse these statistically in an attempt to describe the phenomenon mathematically and in a later paper it is hoped to investigate the possible influence of meteorological factors. In order to analyse such data, which clearly involve both a random or stochastic element of some kind and also some form of serial dependence, it is necessary to use the theory of stochastic processes on which much research has recently been done by mathematical statisticians. Such work has been mainly theoretical and not very many numerical analyses have been made of such phenomena occurring naturally, the best and most complete being an analysis of the sunspot cycle by Yule (1927) in a classic paper which provided the stimulus for much of the later development of the theory. It is hoped that the present paper will help to contribute towards this subject.

In a previous paper (Moran 1952) an analysis has been made of game bird records in Scotland in which stochastic processes, of a somewhat simpler type than those used in the present paper, were found to give a satisfactory fit to series of bags of game birds of four different species over a period of 73 years. That investigation showed that the four species (grouse, ptarmigan, caper, and blackgame), although apparently ecologically independent, showed strong correlations in population size between each other. They also showed strong serial correlation in the sense that one year's population was strongly correlated with the previous year's. The fact that the series were *serially* correlated meant that the ordinary statistical test of a correlation coefficient could not be applied since

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the mathematical assumptions of such a test were not satisfied. It was therefore necessary to investigate the internal structure of each series and then apply an approximate test for correlation between such series, which was devised by Bartlett (1935). No evidence of any tendency to a cyclic oscillation was found.

In the present paper we are not concerned with testing correlations between two series but are attempting to find a representation of the process generating the series. This will enable us to set up prediction formulae which are, in a certain sense, optimal. In a later report I hope to discuss whether the data are correlated with meteorological factors and so determine whether the latter can be invoked to explain why the cycles in the numbers of lynx occur with almost perfect synchronization over the whole of Canada.

II. Treatment of the Catch Records

The records used are given in Elton and Nicholson (1942). When the total captures for the whole area are considered for each year, a rather blurred picture of the cycle appears, but on splitting up the records into the individual regions, the cyclic behaviour of the population in each region and the very strong synchronization between even widely separated areas becomes quite clear. The only region in which complete figures are available over a long period of years is the Mackenzie River district, there being gaps (in particular for 1892-1896) for all the other series. The records of this district were therefore chosen for analysis and cover the years 1821-1934 inclusive. Maps of the districts are given in Elton and Nicholson's paper and these show that at various times changes have taken place in their definition and geographical extent. This appears, surprisingly enough, to have had no observable effect on the records. The actual trapping numbers are given in the second column of Table 6 and are reproduced by permission of Mr. Charles Elton.

We regard these trapping records as giving proportionate estimates of the total population. As this is not an exact method of estimating relative population density we are introducing a statistical error of estimation whose effect will be discussed later but which appears to be small. We would also expect that over this long period of time there would have been changes in the number of trappers engaged and in the methods used, which would introduce a long-term trend or change in the average of the numbers caught, but again, of this there appears to be no evidence.

The cycle is very asymmetrical with a very sharp and large peak and a relatively smooth and small trough. The range in this series is from 39 to 6,991 skins. As the variable in the stochastic processes we intend to apply to this problem varies in a more or less symmetric manner about its mean it was decided to transform the data by taking logarithms (to the base 10). The resulting series is given in Table 6 and has been graphed in a previous paper (Moran 1949). To the eye, at least, it seems that the transformation gives a series which appears to vary symmetrically about its mean. We therefore proceed with the transformed data. Further discussion of the effect of this transformation will be given later. We write y_t for the actual number trapped in year t and $x_t = \log_{10} y_t$.

The two main problems which now confront the biologist are to explain why this clearly marked oscillation occurs, and to explain why it occurs in synchronization over the whole of Canada. No plausible theory which will answer both these questions has yet been put forward.

One type of theory suggests that the population density is directly and strongly dependent on some meteorological or other terrestrial phenomenon *which itself shows definite oscillations* and that these oscillations induce those of the population. An example of such a theory is the idea that the lynx cycle was related to the sunspot cycle. Examination of the data shows that this is impossible (Moran 1949) since the cycles are sometimes in phase and sometimes completely out of phase. Other meteorological phenomena have been put forward but it does not seem that there is, as yet, any clear evidence of such a governing cycle. However, one advantage of this type of theory is that it would also explain the synchronization.

Alternatively it may be supposed that the oscillations arise from the population dynamics of the lynx themselves. It is known that the main food of the lynx is the snowshoe rabbit and that such a predator-prey relationship can easily result in an oscillatory process. However, random influences will affect the process and such random effects will show themselves not merely as superimposed errors in the series of observations but will affect the future course of the cycle and thus become incorporated into the future history of the series. It follows that meteorological influences, even if not serially correlated and not themselves showing any cyclic behaviour, might well account for the synchronization of the lynx cycle over the whole of Canada provided they themselves act more or less uniformly over the area. It is hoped to investigate this possibility in a later paper.

Turning now to the mathematical representation of the data, two models suggest themselves. If the explanation of the cycle is of the first type of theory described above, and if in addition the cyclic phenomenon causing the lynx cycle follows a strict mathematical cycle, one suitable model of the observations would be to suppose that

$$x_t - m = a \sin (bt - c) + \epsilon_t, \quad \ldots \quad \ldots \quad \ldots \quad (1)$$

where m is the mean of the series, a, b, and c are constant, and ε_t is a sequence of independent random variables which may be described as 'error.' If the cycle was not of a simple sine wave type further trigonometric terms might be added. The essential feature of this model is that the random element at any given time does not influence the future course of the cycle.

Alternatively, if the lynx cycle is to be explained by the second type of theory above, or if the causal cycle in the first theory is not a strict cycle but some kind of random process, a suitable model will itself have to be some kind of random or stochastic process. Such models of stationary stochastic processes have been extensively studied by statisticians ever since Yule's classical paper (1927) on the analysis of the sunspot cycle. A suitable model is obtained by supposing that the series of values of x_t is generated by a relationship of the form

$$x_t - m = a_1(x_{t-1} - m) + a_2(x_{t-2} - m) + \ldots + a_k(x_{t-k} - m) + \epsilon_t , \quad .. \quad (2)$$

where m is the mean of the process, $a_1, \ldots a_k$ are constants, and ϵ_t is a sequence of independent random variables with zero means and the same standard deviation. In such a case the random element ϵ_t is itself incorporated into the future course of the process. Such a relationship is known as an autoregressive or linear stochastic difference equation. If such a process can be reasonably regarded as a good representation of the system generating the observed data, and if the oscillations are due to an intrinsic oscillatory tendency in the biological system itself then the synchronization of the cycles over the whole of Canada might well be due to the correlation between the weather at different places, even though there is no intrinsic cycle in the weather itself. This could be investigated by seeing how strongly the residuals calculated from (**2**) are correlated with various meteorological phenomena.

To determine statistically what model best fits the observed data we now carry out a correlogram analysis. The series of x's has a mean $\bar{x} = 2.9036$ and appears to be trend-free. If we split the series into two halves, 1821-1877 and 1878-1934, we get means 2.9111 and 2.8961. Unfortunately no test of significance of the difference of these means is possible because not only are they correlated but they are themselves based on a series of correlated terms. In order, therefore, to calculate the standard error of their difference it would be necessary to know the serial correlations in the series and the estimation of these requires the assumption that the series is trend-free. No doubt an approximate test would be possible but the agreement is so close that this does not seem necessary. The general problem of testing for trend in a series of correlated terms is one which urgently requires the attention of mathematical statisticians. This absence of trend is very remarkable when one remembers that the geographical area covered by the term 'Mackenzie River District' has changed somewhat in the course of time (see the maps given in Elton and Nicholson 1942). Moreover, with the development of Canada between 1821 and 1934 one would expect that the intensity and efficiency of trapping would have changed.

There being no evidence of trend one can proceed to calculate the standard deviation and serial correlations in the ordinary way. The standard deviation was found to be 0.55737. The serial correlation coefficients, r_s, of orders $s = 1, 2, \ldots 27$ were found from the formula

$$r_s = \frac{n}{n-s} \frac{\sum_{i=1}^{n-s} x_i x_{i+s} - \frac{1}{n-s}\left(\sum_{i=1}^{n-s} x_i\right)\left(\sum_{i=s+1}^{n} x_i\right)}{\sum_{i=1}^{n} x_i^2 - \frac{1}{n}\left(\sum_{1}^{n} x_i\right)^2} , \quad .. \quad .. \quad (3)$$

where

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n} x_i = 2{\cdot}9036 \text{ and } n = 114.$$

The factor $n(n-s)^{-1}$ is introduced because the numerator is based on $n-s$ pairs of values and the denominator on n values. Taking into account the cor-

rections for the means we might well have used $(n-1)(n-s-1)^{-1}$ instead but the difference appears to be negligible. The results of this calculation, which was carried out for me by the computing staff of the Oxford Institute of Statistics, are shown in Table 1.

TABLE 1

VALUES OF r_s FOR $s = 1, 2, \ldots 27$

s	r_s	s	r_s
1	0·79516	15	−0·70538
2	0·34788	16	−0·47523
3	−0·13596	17	−0·08560
4	−0·51332	18	0·30214
5	−0·65116	19	0·54795
6	−0·51696	20	0·54308
7	−0·16895	21	0·26726
8	0·25296	22	−0·14559
9	0·58422	23	−0·50129
10	0·66419	24	−0·64342
11	0·42315	25	−0·53101
12	−0·01529	26	−0·21046
13	−0·43674	27	0·19955
14	−0·69531	—	—

When r_s is plotted against s we obtain a "correlogram," which is here a smooth, oscillating curve which appears to be very slowly decreasing in amplitude. We are now in a position to fit to the data a model of the form (2). We must first decide on the value of k. To do this we calculate the partial serial correlation coefficients and test their significance in the manner indicated by Quenouille (1949). The idea of using partial serial correlation coefficients in this situation is due to Yule (1927). By $r_{13,\,2}$ he denotes the observed correlation between x_t and x_{t-2} when the effect of x_{t-1} is removed. Similarly he denotes by $r_{14,\,23}$ the observed correlation between x_t and x_{t-3} when the effect of x_{t-1} and x_{t-2} are removed, and so on. It is not difficult to show that

$$r_{1k\cdot 23\ \ldots} = \frac{\begin{vmatrix} 1 & r_1 & r_2 & \ldots & r_{k-2} & r_1 \\ r_1 & 1 & r_1 & & r_{k-3} & r_2 \\ \cdot & \cdot & \cdot & \ldots & \cdot & \cdot \\ r_{k-1} & r_{k-2} & r_{k-3} & & r_1 & r_k \end{vmatrix}}{\begin{vmatrix} 1 & r_1 & r_2 & \ldots & r_{k-2} & r_{k-1} \\ r_1 & 1 & r_1 & \ldots & r_{k-3} & r_{k-2} \\ \cdot & \cdot & \cdot & \ldots & \cdot & \cdot \\ r_{k-1} & r_{k-2} & r_{k-3} & \ldots & r_1 & 1 \end{vmatrix}} \quad \ldots \quad (4)$$

Moreover, it is not difficult to see that this is in fact equal to a_{k-1} in the fitting, by least squares, of a regression formula of the type

$$x_t = a_1 x_{t-1} + \ldots + a_{k-1} x_{t-k+1} + \epsilon_t.$$

Carrying out the calculations we obtain Table 2.

TABLE 2
VALUES OF THE PARTIAL SERIAL CORRELATIONS

Suffix of r	r	5% Level
1	0·79516	0·1820
13,2	−0·77341	0·1828
14,23	−0·07810	0·1836
15,234	−0·25037	0·1844
16,2345	0·19955	0·1852
17,23456	0·06076	0·1860

Quenouille (1949) has shown that such a partial serial correlation coefficient can be tested for significant deviation from zero in the ordinary manner provided three 'extra' degrees of freedom are allowed. In the third column of Table 2 we have therefore calculated $1.96\ (n+3-p)^{-\frac{1}{2}}$ where $p = 1, \ldots 6$. This should be very close to the true 5 per cent. significance level. It will be seen that r_1 and $r_{13,\,2}$ are both highly significant whilst $r_{13,\,234}$ and $r_{16,\,2345}$ would both also be judged significant. It is curious that Yule (1927) should have found the same partial serial correlations to be large when he calculated them for his series of graduated sunspot numbers (but not for the ungraduated series). Table 2 therefore suggests that k should be taken as 2. There is clearly no advantage in taking it as 3 and if we took it as 5 to include the effect of terms which are apparently significant in Table 2 the reduction in the variance of the estimated residuals would be quite small. Changing the notation slightly to agree with conventional practice in dealing with three-termed autoregressive series we therefore fit a relation of the form

$$x_t - m = a(x_{t-1} - m) + b(x_{t-2} - m).$$

We then find

$$a = \frac{r_1(1-r_2)}{1-r_1^2} = 1{\cdot}4101,\ b = \frac{r_2 - r_1^2}{1-r_1^2} = -0{\cdot}7734,$$

and our estimated generating relationship for the process is

$$x_t - 2{\cdot}9036 - 1{\cdot}4101(x_{t-1} - 2{\cdot}9036) - 0{\cdot}7734(x_{t-2} - 2{\cdot}9036). \quad \ldots \ (5)$$

We can estimate the variance of the error term ϵ_t by the relation (Kendall 1946*b*, p. 438),

$$\text{var}\ (\epsilon_t) = \text{var}\ (x_t)\ \frac{(1+b)\ \{(1-b)^2 - a^2\}}{1-b}$$
$$= 0{\cdot}04591.$$

If we calculate what the theoretical form of the correlogram should be, assuming the first two serial correlations to have their observed values, we get

a smooth curve which oscillates in the same manner as the empirical correlogram but is much more heavily damped. This wide apparent divergence between the amplitudes of the oscillations in empirical and theoretical correlograms has been repeatedly noticed before in experimental sampling studies (see e.g. Kendall 1946*a*). No attempt has been made here to carry out the goodness of fit test of the correlogram devised by Quenouille since it was thought that the tests in Table 2 were sufficient.

It is somewhat more difficult to say how far Table 1 enables us to discriminate between a model of the type of equation (**1**) (a model of 'concealed periodicities') and a model of the type of equation (**2**). If the model was of the former type, and no further periodic terms were involved, the observed correlogram should approximate to the form

$$r_s = a \cos s\beta,$$

where a and β are constant and $|a| < 1$. In this case there would be no damping and r_s could never be larger than a except for $s = 0$. It would seem from Table 1 that there is a genuine, if small, amount of damping and moreover r_1 seems definitely larger in absolute value than any of the subsequent peaks or troughs. It would therefore seem that the autoregressive model is somewhat more plausible. This is just what we would expect if the cyclic behaviour arises from factors endogenous to the biological system.

TABLE 3
ONE-YEAR PREDICTIONS OF x_t

Year	x_t	Predicted x_t	Error
1927	3·187	3·197	−0·010
1928	2·723	2·867	−0·144
1929	2·686	2·430	0·256
1930	2·821	2·737	0·084
1931	3·000	2·956	0·044
1932	3·201	3·103	0·098
1933	3·424	3·249	0·175
1934	3·531	3·407	0·124

Formula (**5**) can also be used as a prediction formula and is an optimal one in the least squares sense. To see how it works in practice predictions of x_t were made for the years 1927-1934, each prediction being based on the observed values for the two preceding years. These are given in Table 3, together with the actual error of prediction. In Table 6 will be found all the residuals calculated from formula (**5**) and these are in fact the errors of prediction. The error in the prediction may be compared with the standard deviation of the distribution of ε_t, as found above, which is $\sqrt{0.04591} = 0.2143$. This error of prediction assumes that the values of m, a, and b are exact, which is not true since they have been estimated—but this should introduce only a rela-

tively small error. It may also be noticed that the prediction formula (**5**) has been calculated from data which include the data used in Table 3 as an illustration but it is not thought that this is of any consequence.

The results of Table 3, when converted into actual catches of lynx, are given in Table 4.

TABLE 4
PREDICTED CATCH

Year	y_t	Predicted y_t
1927	1537	1574
1928	529	736
1929	485	269
1930	662	546
1931	1000	904
1932	1590	1268
1933	2657	1774
1934	3396	2553

To predict further ahead than 1 year one simply applies formula (**5**) repeatedly, first on the two observed values (e.g. those for 1925, 1926), then on the observed value for 1926 and the predicted value for 1927, and so on. Table 5 shows such results for 1927-1934.

TABLE 5
PREDICTIONS OF x_t

Year	x_t	Predicted x_t	Error	S.E. Prediction
1927	3·187	3·197	−0·010	0·214
1928	2·723	2·881	−0·158	0·370
1929	2·686	2·645	0·041	0·453
1930	2·821	2·557	0·264	0·472
1931	3·000	2·615	0·193	0·473
1932	3·201	2·764	0·437	0·488
1933	3·424	2·931	0·493	0·514
1934	3·531	3·050	0·479	0·531

These predictions would, if prolonged, show oscillations which damp away to the mean value of x_t, thus reflecting the uncertainty in the phase for predictions a long way ahead. The standard error of such a prediction can be easily calculated (for details see Stone 1947) and gradually increases to a value equal to the standard deviation of the original series.

III. Discussion

It will be seen that the above predictions, even for 1 year ahead, are not very good. This is somewhat disappointing, especially when we remember that this is an optimal linear prediction method in the sense of least squares. The results of Table 3 may suggest at first sight that there is some kind of systematic behaviour in the signs of the residuals. (This, if true, would perhaps suggest that the process would be better represented by some kind of non-linear model.) To check this, the residuals for the whole series were calculated and are given in Table 6. There is no evidence of any systematic behaviour in the signs of the residuals. However, one curious feature deserves notice. There are 112 residuals and the sum of their squares is 5.788; 56 of these residuals correspond to values of x_t greater than the mean 2.9036 (actually 2.904 was the value used in the calculation of the residuals) and 56 correspond to values of x_t less than 2.9036. However, the sum of squares of the former is equal to 1.781 whilst the sum of squares corresponding to the latter is 4.007. The ratio is 2.250 which would be judged significant at the 1 per cent. level if the two sets could be regarded as random samples from the same normal population, which is not strictly true. Nevertheless this appears to provide strong evidence that our process is not strictly symmetrical, which is not very surprising.

We must also remember that the population of lynx is not exactly proportional to the number caught. A better representation would perhaps be obtained by adding to the series generated by (**5**) an additional "error of observation." The fitting of processes defined in this manner is a much more difficult matter. However, we may shortly indicate here what might be the effect on the serial correlations. If there is an observational error of variance σ^2 in the number caught y_t, then to a first approximation the variance of the error of observation in $x_t = \log_{10} y_t$ will be

$$\left(\frac{\mathrm{d}}{\mathrm{d}y_t}\log_{10} y_t\right)^2 \sigma^2 = \left(\frac{0{\cdot}4343}{y_t}\right)^2 \sigma^2.$$

This error will contribute to the variance of the series and thus to the denominator of the expression for the serial correlation but it will not contribute to the expectation of the numerator. If we assume that the observational error is that of a Poisson distribution, which is not implausible, we would put $\sigma^2 = y_t$. We should therefore subtract the average value of

$$\frac{(0{\cdot}4343)^2}{y_t}$$

from the estimate of the variance in the denominator of the expression for r_t, or what comes to practically the same thing, multiply each r_t by

$$\frac{0{\cdot}31064}{0{\cdot}31064 - (0{\cdot}4343)^2 E\left(\frac{1}{y_t}\right)}.$$

TABLE 6

YEAR (COLUMN 1), NUMBER OF LYNX TRAPPED (x) (COLUMN 2), $y = \log_{10} x$ (COLUMN 3), AND RESIDUALS FROM FORMULA (5) (COLUMN 4)

1	2	3	4	1	2	3	4
1821	269	2·430	—	1878	299	2·476	−0·198
1822	321	2·506	—	1879	201	2·303	−0·017
1823	585	2·767	0·057	1880	229	2·360	−0·028
1824	871	2·940	−0·079	1881	469	2·671	0·069
1825	1475	3·169	0·108	1882	736	2·867	−0·129
1826	2821	3·450	0·200	1883	2042	3·310	0·278
1827	3928	3·594	0·125	1884	2811	3·449	−0·057
1828	5943	3·774	0·319	1885	4431	3·646	0·283
1829	4950	3·695	0·098	1886	2511	3·400	−0·128
1830	2577	3·411	0·065	1887	389	2·590	−0·439
1831	523	2·718	−0·289	1888	73	1·863	−0·214
1832	98	1·991	−0·259	1889	39	1·591	−0·088
1833	184	2·265	0·504	1890	49	1·690	−0·168
1834	279	2·446	−0·263	1891	59	1·771	−0·436
1835	409	2·612	−0·140	1892	188	2·274	0·029
1836	2285	3·359	0·513	1893	377	2·576	−0·316
1837	2685	3·429	−0·343	1894	1292	3·111	0·182
1838	3409	3·533	0·241	1895	4031	3·605	0·155
1839	1824	3·261	−0·124	1896	3495	3·543	−0·189
1840	409	2·612	−0·309	1897	587	2·769	−0·494
1841	151	2·179	−0·037	1898	105	2·021	−0·199
1842	45	1·653	−0·455	1899	153	2·185	0·422
1843	68	1·832	0·131	1900	387	2·588	0·015
1844	213	2·328	−0·033	1901	758	2·880	−0·134
1845	546	2·737	−0·184	1902	1307	3·115	0·001
1846	1033	3·014	−0·100	1903	3465	3·540	0·319
1847	2129	3·328	0·140	1904	6991	3·845	0·207
1848	2536	3·404	−0·013	1905	6313	3·800	0·061
1849	957	2·981	−0·300	1906	3794	3·579	0·140
1850	361	2·557	−0·069	1907	1836	3·264	0·101
1851	377	2·576	0·221	1908	345	2·538	−0·352
1852	225	2·352	−0·357	1909	382	2·582	0·472
1853	360	2·556	0·176	1910	808	2·907	0·174
1854	731	2·864	0·024	1911	1388	3·142	−0·015
1855	1638	3·214	0·097	1912	2713	3·433	0·195
1856	2725	3·435	0·063	1913	3800	3·580	0·114
1857	2871	3·458	0·045	1914	3091	3·490	0·042
1858	2119	3·326	0·052	1915	2985	3·475	0·268
1859	684	2·835	−0·236	1916	3790	3·579	0·323
1860	299	2·476	−0·005	1917	674	2·829	−0·585
1861	236	2·373	0·020	1918	81	1·909	−0·367
1862	245	2·389	−0·097	1919	80	1·903	0·344
1863	552	2·742	0·153	1920	108	2·033	−0·229
1864	1623	3·210	0·136	1921	229	2·360	−0·094
1865	3311	3·520	0·060	1922	399	2·601	−0·210
1866	6721	3·828	0·292	1923	1132	3·054	0·156
1867	4245	3·628	−0·103	1924	2432	3·386	0·036
1868	687	2·837	−0·373	1925	3574	3·553	0·085
1869	255	2·406	0·156	1926	2935	3·468	0·022
1870	473	2·675	0·421	1927	1537	3·187	−0·010
1871	358	2·554	−0·412	1928	529	2·723	−0·144
1872	784	2·894	0·307	1929	485	2·686	0·256
1873	1594	3·202	0·041	1930	662	2·821	0·084
1874	1676	3·224	−0·108	1931	1000	3·000	0·044
1875	2251	3·352	0·227	1932	1590	3·201	0·098
1876	1426	3·154	−0·135	1933	2657	3·424	0·175
1877	756	2·878	−0·033	1934	3396	3·531	0·124

I have not attempted to calculate $E\left(\frac{1}{y_t}\right)$ but the insertion of typical values shows that the effect on the estimated serial correlations is small. It is true that the observational error is probably larger than that given by assuming a Poisson distribution but it seems likely that this effect is not large.

Summing up therefore we may say that the series of logarithms of the observed catches is well fitted by an autoregressive scheme and that the data are at least consistent with the idea that the cyclic behaviour is due to factors intrinsic to the biological system. There remains to be explained the synchronization between widely separated areas. To this question I hope to return in a later paper.

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THE LOTKA-VOLTERRA THEORY OF INTERSPECIFIC COMPETITION

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Summary

It is shown that there is a fundamental contradiction in the mathematical theory of interspecific competition of Lotka and Volterra.

I. Introduction

Anyone who reads the literature on animal ecology will have noticed that most biologists now seem to accept the theory that the numbers of animals in nature are determined by "density-dependent factors" (Smith 1935; Elton 1949). Broadly, according to Elton, there are two categories of density-dependent factors, namely, parasites and predators, and competition. Competition is further subdivided into intraspecific and interspecific competition. The study of interspecific competition has been profoundly influenced by a mathematical theory which is usually attributed to Lotka (1925, 1932) and Volterra (1926, 1931). We shall show below that there is a fundamental contradiction in the theory which seems hitherto to have been missed both by its exponents (e.g. Gause 1934, 1935; Gause and Witt 1935; Crombie 1945) and its critics (Smith 1952). We are preparing a criticism of the whole theory of "density-dependent factors" which we shall publish elsewhere. In the meantime this paper deals only with this particular aspect of the theory.

II. Theory of Lotka and Volterra

The essentials of the theory may be stated briefly—it is assumed that when a population of animals, all of the same kind, are increasing in a place where food and space are finite and constant it will obey two simple laws:

(*a*) The relative rate of increase (i.e. the mean rate of increase per individual) decreases from a maximum (r) to zero as the density of the population increases from very few to saturation (K).

(*b*) The relationship between rate of increase and density is assumed to be linear throughout this range.

Certain concomitant assumptions which we mention without further discussion, except to say that they seem rather unrealistic, are:

(*c*) Every individual at every stage of its life cycle is exactly equivalent to every other individual.

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(*d*) Each individual begins to exert its full influence the moment it is added to the population.

(*e*) The population has a stable age distribution.

Granted all these assumptions we may write the equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \quad .. \quad .. \quad .. \quad (1)$$

where N is the density of the population at time t and r is a constant called the innate capacity for increase. It is theoretically the rate at which a population of stable age distribution will increase when density is optimum (Birch 1948).

When populations of two species whose requirements for food or space are similar live together in a place where space and food are finite and constant one additional assumption is made:

(*f*) The numbers of either species may be expressed in terms of the other by multiplying one of them by a constant.

Thus, if at any moment of time there are N_1 individuals of species A and N_2 individuals of species B, there will be a particular number which we may call M_1 which will represent the number of species B expressed as the number of species A which would have the equivalent effect on the rate of increase of species A. We may then write $M_1 = \alpha N_2$ and similarly $M_2 = \beta N_1$. The theory of Lotka and Volterra assumes that α and β are positive and constant for all possible values of N_1 and N_2. Given this one additional assumption we may rewrite equation (**1**) as follows:

$$\frac{dN_1}{dt} = r_1 N_1\left(1 - \frac{N_1 + \alpha N_2}{K_1}\right), \quad .. \quad .. \quad .. \quad (2)$$

$$\frac{dN_2}{dt} = r_2 N_2\left(1 - \frac{N_2 + \beta N_1}{K_2}\right). \quad .. \quad .. \quad .. \quad (3)$$

When the density of neither population is changing any more, that is, when $dN_1/dt = 0 = dN_2/dt$, it is said that "the system has reached equilibrium." If there were no restriction on the numerical values possible for the quantities $(N_1 + \alpha N_2)$ and $(N_2 + \beta N_1)$ then there would be three different ways in which equilibrium might be reached. These are: (*a*) as N_1 approaches zero and N_2 approaches the asymptote K_2; (*b*) as N_2 approaches zero and N_1 approaches the asymptote K_1; (*c*) N_1 and N_2 both remain above zero and approach asymptotes which will be less than K_1 and K_2 respectively. If all three ways of approaching equilibrium are accepted as theoretically possible it is possible to derive a set of four inequalities which describe the circumstances in which each particular state of equilibrium may be realized. These inequalities were indicated by Lotka (1925, 1932) and Volterra (1926, 1931), expressed rather more explicity by Gause and Witt (1935), and repeated by Crombie (1945) and Hutchinson and Deevey (1949). The set of four inequalities and the limits, as equilibrium is approached, which they determine for N_1 and N_2 are:

(i) When

$$\frac{\alpha}{K_1} < \frac{1}{K_2} \text{ and } \frac{\beta}{K_2} < \frac{1}{K_1},$$

then

$$\text{limit } N_1 = \frac{K_1 - \alpha K_2}{1 - \alpha\beta} \text{ and limit } N_2 = \frac{K_2 - \beta K_1}{1 - \alpha\beta}, \text{ as } t \to \infty.$$

(ii) When

$$\frac{\alpha}{K_1} < \frac{1}{K_2} \text{ and } \frac{\beta}{K_2} > \frac{1}{K_1},$$

then

$$\text{limit } N_1 = K_1 \text{ and limit } N_2 = 0, \text{ as } t \to \infty.$$

(iii) When

$$\frac{\alpha}{K_1} > \frac{1}{K_2} \text{ and } \frac{\beta}{K_2} < \frac{1}{K_1},$$

then

$$\text{limit } N_1 = 0 \text{ and limit } N_2 = K_2, \text{ as } t \to \infty.$$

(iv) When

$$\frac{\alpha}{K_1} > \frac{1}{K_2} \text{ and } \frac{\beta}{K_2} > \frac{1}{K_1},$$

then

$$\text{limit } N_1 = 0 \text{ or } K_1 \text{ and limit } N_2 = 0 \text{ or } K_2, \text{ as } t \to \infty.$$

This then is the theory as it relates to interspecific competition. It has had a powerful influence on ecological thought. In the view of Hutchinson and Deevey (1949) "The generalization implicit in cases (2) and (3) (i.e. our inequalities (ii), (iii), and (iv)) that two species with the same niche requirements cannot form mixed steady-state populations in the same region, has become one of the chief foundations of modern ecology."

III. Examination of the Theory and Conclusions

Let us look a little more closely at the origin and implications of these inequalities. We started with the clear understanding that α is a constant which converted N_2 to units which are additive to N_1 so that $N_1 + \alpha N_2$ in equation (**2**) is equivalent to N in equation (**1**). Now the solution of equation (**1**) shows that N approaches K as t tends to infinity but never exceeds K, and dN/dt approaches zero as a limit but never becomes negative. Thus K is conceived as the maximum or saturation density for the particular place and the particular circumstances in which the population is living.

The same concept is carried over to equations (**2**) and (**3**) but in the general solution of these equations $N_1 + \alpha N_2$ may exceed K_1 and $N_2 + \beta N_1$ may exceed K_2. So the concept of K must be modified; instead of representing a true maximum density, K now represents a particular density which may be exceeded so long as two species are living together but not when only one

remains. The absurdity, on biological grounds, of this conception is immediately clear, especially when it is recalled that the two species are, by hypothesis, such that they interfere with each other to each other's detriment and α is defined as a constant which makes αN_2 numerically equivalent to N_1.

We must therefore discard as unacceptable, because it is nonsensical, any solution to equations (**2**) and (**3**) which implies that $N_1 + \alpha N_2$ may exceed K_1 or $N_2 + \beta N_1$ may exceed K_2. Equation (**2**) may be rewritten in the form:

$$\frac{dN_1}{dt} = r_1 N_1 - r_1 N_1 \left(\frac{N_1 + \alpha N_2}{K_1} \right), \qquad .. \quad .. \quad (4)$$

from which it is immediately apparent that if r_1 and α are positive (which they must be) and $N_1 + \alpha N_2$ cannot exceed K_1, then dN_1/dt can never be less than 0. In other words, there is no provision in this equation for the density of the population of species A (N_1) to become smaller. It may increase or it may remain stationary but it may not decline; similarly with species B. The equations therefore cannot be used to predict any state of equilibrium which requires either N_1 or N_2 to approach zero. The last three inequalities must be discarded on these grounds, leaving only the first, from which it must be concluded that once the two species have come together they must continue to live together indefinitely. This also is rather nonsensical and we reach the general conclusion that these mathematical models with their unrealistic initial assumptions are quite unlike nature. They are more likely to mislead than help in the interpretation of observations and measurements of natural populations.

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SOME ASPECTS OF THE BIOLOGY OF THE MOUND ANT *IRIDOMYRMEX DETECTUS* (SMITH)

By A. H. Duncan-Weatherley*

[*Manuscript received September* 19, 1952]

Summary

Counts of foragers of *Iridomyrmex detectus* (Smith) leaving the nest during the day revealed, over a 4-month period, bimodal diurnal activity patterns under natural conditions. It is likely that the patterns are basically endogenous, modified by environmental factors. The number of ants active in a foraging trail at any time decreases with distance from nest and the trails are often impermanent, though some lasted almost unchanged for 4 months.

Nests were made from excavated earth and capped with a variety of materials. The behaviour on the nest surface mostly consisted of apparently random wandering which sometimes resulted in the ant leaving the nest, and sometimes its return to its hole of emergence or to another hole.

The uncoordinated behaviour of the ants when the nest is molested and the inefficient way in which they handle objects and carry food and building materials, are suggestive of an unspecialized type of behaviour life. Attempts to reverse the orientation of the ants have shown how difficult this is and the possibility that smell and sight govern orientation has been discussed.

Territoriality among nests is described together with a phenomenon of "common trails," thought to represent still-existing links between parent and "branch" nests.

I. Introduction

Iridomyrmex detectus (Smith), a member of the subfamily Dolichoderinae (Wheeler 1926), is a rather large, dark red ant with a faintly iridescent sheen.

Besides the typical variety of Smith with which this paper deals, there are at least two other varieties (var. *sanguinea* Forel, and var. *viridaeneus* Viehmeyer; see Part 6 of the Catalogue of the Hymenoptera in the British Museum). The variety under discussion will be referred to henceforth, in this paper, as *I. detectus*.

I. detectus is widely distributed through Australia, building large and characteristically mound-shaped nests. Brief accounts of these and some other aspects of its natural history will be found in Froggatt (1907), McKeown (1942), and Brewster, Brewster, and Crouch (1946).

This report embodies only work carried out over the period early January to early April 1951. Consequently, the observations, while presumably accurate for the locality and period of the year in which they were recorded, should not, without further data of a corroborative nature, be regarded as generally completely true for this variety.

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The site of the work was in and around a public reserve at Thornleigh, a suburb of Sydney, N.S.W.

II. Diurnal Activity

This ant is almost exclusively diurnal in its foraging. Although at almost any time of day or night ants were active on the surface of the nest, their traffic to and from the nest was restricted to daylight hours. The activity on the nest surface at night is, however, very low.

The ants move principally along trails radiating from the nests. In western New South Wales the trails are clearly defined ribbons of bare ground through the grass. At Thornleigh, however, because most of the ground was bare, stony, and largely devoid of grass, the trails were distinguished by the numbers of ants employing them, i.e. their "popularity" as pathways.

In this investigation it was felt that an appropriate manifestation of the activity of an ant nest during the day would be the frequency of ants leaving it at any given time. This method has been employed for the honeybee (Butler and Finney 1942).

The side boundaries of many of the trails at Thornleigh were difficult to define. That is, while most of the ants moving in a trail away from the nest could be contained in a band, say, a foot wide, there were those ants which, while travelling obviously in the same direction as the majority, were nonetheless more than 6 in. on either side of the "centre line" of the trail. These ants would not necessarily be continuously outside the popular zone, but while travelling in its general direction, might spend part of their time in it and part outside. Three of the four trails used for activity counts were like this, and because their width did not permit accurate counts it was necessary to limit it by drawing a line, about 2 yd. from the point of issue of the trail from each nest at right angles to and across the trail. This had the following effect: those ants which actually occupied the trail proper were in the majority and were counted (the centre of the limiting line being at the centre of the trail). Some of those which strayed from the more popular part of the trail were not counted (as they passed beyond the extremities of the line) and some which had strayed but returned, or later were to stray, were counted—in other words, these roughly balanced each other. Still others were permanently outside this popular zone and were not counted. Although the number of ants thus counted was not so high as the absolute number using the trail, it was possible, by this method, to escape from the difficulty of deciding whether or not individual ants were "in the trail" or not. There is no reason to believe that relative changes in activity through the day would be distorted by this method of counting.

I. detectus leave and enter their nests by random routes as well as by main routes, but because of the relatively small numbers and the wide range of their exits and entries they are unsuitable for activity counts.

An experiment (12.i.51) gives some quantitative indication of the numbers leaving and entering by random routes as compared with trails. Lines were drawn (Fig. 1) through trails 1 and 2, nest I, and four more lines were drawn, arranged as shown, around the nest. The lines were all about 2 yd. out from

the nest margin and about 2 yd. long, except those across trails 1 and 2, which were 2 ft. long. Three-minute counts at all six lines gave the data in Table 1.

TABLE 1
TRAFFIC IN TRAILS COMPARED WITH RANDOM TRAFFIC

Line Number	Number of Ants Crossing Line in 3 Min.
1	44
2	28
3	0
4	1
5	1
6	0

Thus it may be seen that only insignificant numbers did not travel by main trails.

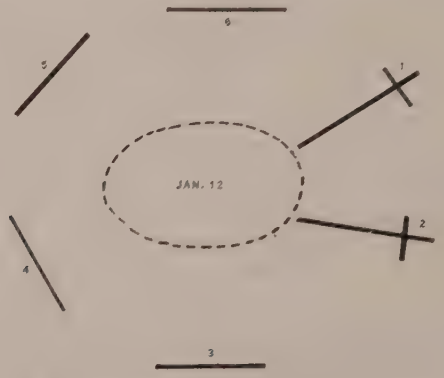

Fig. 1.—Distribution of counting lines around nest I, 12.i.1951.

Sites for activity counts were selected close to the nests, because numbers of ants active along the length of a trail at any time generally decreased with increasing distance from the nest. Two factors contribute to this effect. First, many ants branch off the trails on individual foraging excursions (however, they or other ants tend to join the trail again when returning to the nest, because, for the main part of the day, at the 2-yd. mark from the nest, the number of incoming ants roughly equals the number of outgoing at any given time). Obviously if this branching off goes on along the length of the trail the result will be reduction in numbers active in the trail as distance from the nest increases. Second, some ants adhere to the trail, completing their foraging within its confines, so naturally there will be less of this latter class the further one moves along the trail from the nest.

Some trails were impermanent. In Figure 3 the disposition and number of trails around nest I are shown for four consecutive days. Trail 1 was unchanged; indeed, this trail never disappeared or diminished in importance. The establishment of trails was probably determined generally in the first place by the location of sites for food and building materials.

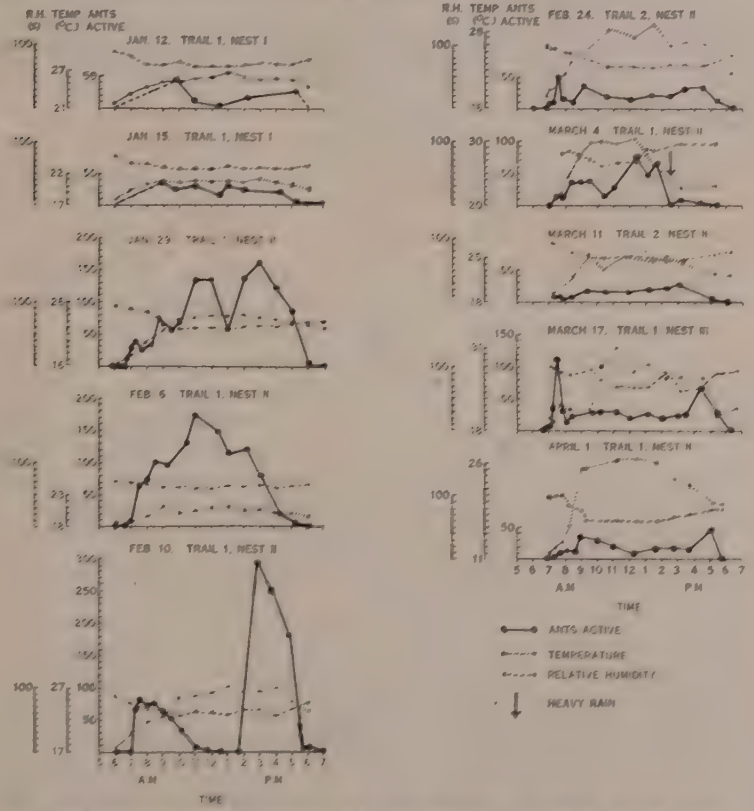

Fig. 2.—Activity, temperature, and relative humidity curves for the trails, nests, and dates indicated. Ants active, as the term is used above, means number of ants crossing the counting line in a trail in 6 min. See Section II.

The relative importance of some main trails was rather less than trail 1, nest I. For instance, while trail 1, nest II, customarily carried the heaviest traffic for that nest, this did not always hold, and sometimes activity in trail 1 began later than in trail 2. In such cases trail 2 was used for activity counts.

For the counts of diurnal activity four trails from three nests were used. Counts were carried out at intervals throughout a day on 10 separate days. On the two days when early morning counts were omitted it seemed reasonable to interpolate lines in the activity curves (based upon the data for subsequent days) to show rough indices of activity for the hours 6 to 9 a.m. inclusive.

These lines are included in Figure 2. Of the 10 days' activity shown in Figure 2, 2 are from trail 1, nest I; 5 from trail 1, nest II; 2 from trail 2, nest II; 1 from trail 1, nest III. All the trails are pictured in Figure 4 and trail 1, nest III, referred to above, is trail 1-1 between nests III and IV.

The method of counting outgoing ants was to count all ants crossing the line laid across the trail in 6 min. The time of day 3 min. after a count was begun was considered to be the time of day for that activity count. The majority of the activity curves in Figure 2 display a tendency for a bimodal distribution of diurnal activity.

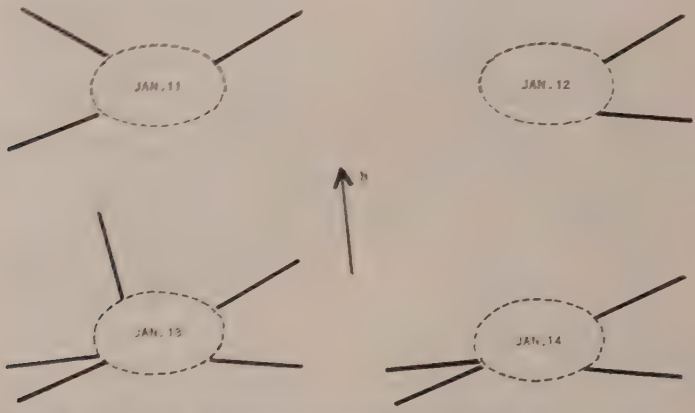

Fig. 3.—Disposition and numbers of trails from nest I on four consecutive days.

III. Climatic Factors

Air temperatures and relative humidities (latter obtained with a sling psychrometer) were determined at intervals throughout the day. Light intensities were measured on several days, but because the method of measurement used proved unsatisfactory, it was decided that insufficient reliance could be placed on the data to include them here. Data were not collected at the site of the observations on Jan. 12, 15, and 29 and Feb. 6 and 10, so data were obtained for temperature and relative humidity on these dates from the Meteorological Bureau, Sydney, approximately 10 miles from Thornleigh. From comparison of data taken at Thornleigh with the Bureau data, it was evident that although there were absolute differences in the changes occurring at both places the general shapes of the temperature and relative humidity curves were similar in both locations.

(*a*) *Temperature*

In general, activity increased with temperature in the early morning and decreased with it in the late afternoon, while in the middle stages of the day the relationship was reversed.

(*b*) *Relative Humidity*

Activity increased with decreasing relative humidity in the early morning and decreased as this increased in the evening. Over the middle part of the day this relationship was reversed.

(*c*) *Rain*

I. detectus were unaffected by light to medium rainfall. In heavy showers activity diminished sharply, sometimes ceasing completely (Fig. 2).

(*d*) *Wind*

Ordinary winds did not noticeably affect activity. The ants are so close to the ground that the effects of all but very strong winds are probably insignificant.

IV. Discussion of Activity

Parker (1926), Kumm and Novis (1938), Bates (1944), and Clark (1949) have reported bimodal diurnal activity patterns for insects.

Whether the (bimodal) activity pattern displayed by *I. detectus* is determined by endogenous or external (climatic) factors, or the interaction of both, is difficult to decide from data collected in the field. It is not very profitable to try to assess correlation strength between activity and climatic variables under uncontrolled conditions. As Butler and Finney (1942) stated, when attempting to evaluate the effect of light intensity on honeybee activity under natural conditions: "- - - there is no doubt of the existence of a positive association between light and bee activity. But this association is of little interest, as the same property would hold for any quantity—no matter how irrelevant—which shows a diurnal cycle.

The real importance of the data lies in their answer to the question: 'Are the deviations of the activity rates of the bees from the trend shown by the diurnal cycle associated with similar deviations in the light intensity?'."

In other words, it is only when activity fluctuations repeatedly correspond with light intensity changes that light could be regarded as having a governing effect on activity.

Because changes in relative humidity and temperature are not as sudden as those for light intensity during the day, it is much more difficult to apply a method such as the above when attempting to assess their respective effects on activity from data collected in the field.

The most that can be said of *I. detectus* is that the rather persistent bimodal tendency in its diurnal activity pattern, because of its appearance under a variety of climatic conditions, is probably basically endogenous. However, because of the variations superimposed on this basic bimodal pattern it is apparently affected and modified by environmental factors.

V. Building and Structure of Nests

Nests were always mound-shaped. Apparently they owe their shape to soil transported by the ants from their excavations—evidently originally below

ground level—and piled up around the openings of the excavations (Froggatt 1907). Although Wheeler (1926) wrote that most mound nests owe their shape both to excavation and accumulation of material collected by the workers from nearby, for *I. detectus* it appeared that most of the deposits being added to the nest at any given moment were from soil excavations.

When sectioned, the nests revealed a series of galleries, irregularly shaped and disposed, with no very special features and going below ground level as well as penetrating the mound. Some of them opened through simple openings directly on to the surface of the mound.

The mounds were generally capped with gravel (McKeown 1942), but it was noticed that the ants often employed many other materials as well. Thus nest I was covered with gravel; nest II with soil crumbs, small twigs, and little pieces of charcoal (there had once been a large wood fire nearby). In loose soil without pebbles, surfaces were observed of soil crumbs alone. In other cases the surface had been covered with shale pebbles.

VI. Behaviour on the Nest Surface

A considerable proportion of the ants active on a nest surface at any time during the daylight hours were carrying soil crumbs; only one crumb per ant at a time. Typically an ant would emerge from a nest opening carrying a soil crumb in its mandibles. Moving sometimes apparently randomly, sometimes in more or less of a straight line, it would travel generally a distance of not less than 6 in. from its hole of emergence to deposit its burden. It would then enter the nest, usually through the same hole, occasionally through another. As a result of this random carrying of the soil away from the nest there is no tendency for the soil to accumulate unduly around it. The mound shape is bestowed upon the nests probably by rain and gravity, tending to move the soil down continually, from the apex over the nest margins.

The movements of the ants not engaged in soil-carrying could be categorized as follows:

(1) Ant would emerge from hole, move around near it, then return to it.

(2) Ant would emerge, move around, then, after variable time, go down another hole.

(3) Ant would emerge, leave nest fairly directly (usually on a trail), or do so after a variable period of wandering.

(4) Ant would merely show head out of hole; then withdraw it.

These behaviour patterns are not easy to understand.

VII. Aggressive Behaviour and Defence of the Nest

Active insects such as small beetles, grasshoppers, and other ants escaped easily if placed on a nest of *I. detectus*, provided the colony had not been excited to its maximum of activity and aggressiveness.

Coordination between sections of a nest population did not appear to be highly developed. A small animal, reasonably fast-moving, if it did not halt or pursue an erratic course, was usually able to pass across a nest, disturbing and exciting only those ants in the immediate vicinity of its path. It required considerably more stimulus than this to spread a wave of excitement over the remainder of the nest. For example on February 24 a millipede was placed on nest II. Very little excitement was manifested by the ants, and the millipede proceeded from the nest, unmolested and almost in a straight line. As it approached the edge of the nest it was forced back repeatedly towards the centre by the writer. Eventually this did result in an increase in the general activity of the ants on the nest; but although excitement was contagious, apparently orientation was not, the increased activity being undirected. Even at the highest peak of their activity the ants were unable to stop the millipede which, although hampered for about 20 sec. on one occasion, was even then able to drag itself away from its antagonists and escape.

Curiously enough, while ants of other species were able to make good their escape, those of the same species but from other nests (except nest VII members placed on nest II) were often attacked (see Sections XIII, XIV).

It should be realized that the "marauders" described above, having been artificially introduced, are not true marauders. Their attempts to escape as quickly as possible would be the reverse, and therefore atypical, of true marauders.

The nearest one could come to observing the mobilization of the nest under actual attack was to stamp on the margin with one's foot, or to disturb the nest with a stick. Under such conditions the ants did respond with more purpose. A group of them would attack the site of the stimulus vigorously, and a wave of excitement would be propagated in all directions over the nest surface. The coordination accompanying the excitement decreased, however, with increasing distance from the site of the stimulus. This held even with the most violent stimuli, when quite a number of ants were destroyed.

Five nests were roughly tested for aggressiveness by the comparative readiness of their colonies to attack the observer when he stood on the fringe of the nest. The relative aggressiveness of the nests was V > IV > III > II > I.

VIII. Handling of Objects

The handling of masses, later to be used as food or building material, was interesting. It is described best by recounting some observations.

A freshly killed small spider was placed on nest II. Some ants examined it cautiously. Finally, two ants secured holds on it. They pulled in nearly opposite directions. Others then secured holds at random, releasing their grips, however, after a few moments. Eventually others attached themselves more permanently and after much apparently random pulling about of the spider, the whole group dragged it awkwardly down a hole.

On another occasion ants were watched handling the adbomen of an earwig on the margin of nest I. They pulled at it in an apparently aimless fashion

for several minutes, but when it was placed on the nest proper it was pulled quickly to the mound top by the two ants still holding to it. When only one ant remained it was reversed so that it pulled downhill. It reoriented itself promptly to pull up the mound. This was repeated twice. A little later, two ants were observed with the same earwig pulling against each other in the way described for the spider.

IX. Carrying of Food and Building Materials

These were always functions of single ants (except sometimes where they occurred on the nest surface).

Incoming foragers only occasionally would be carrying food. This raises the question whether ants forage for themselves or to find food for the nest. While there is ample evidence that the higher subfamilies (of which the Dolichoderinae is one) indulge in the storage of food and feeding of sister ants and larvae by regurgitation (Wheeler 1926), it yet seems possible that members of *I. detectus* feed themselves first before concerning themselves with the requirements of the nest. Pieces of sweet biscuit dropped on nest II were consumed on the spot by the ants without any evident attempt to carry them into the nest; and it was only when large food deposits were located by the foragers that many were seen returning food-laden. However, the ants seemed to have considerable liking for the sap exudate of eucalypts (Fig. 4), growing near the nests, and they probably carried a good deal of this back to the nest for the subsequent regurgitation feeding of their sisters. Building materials, such as pebbles and twigs, were scattered on the nest surface, where they seemed to retard the effect of erosion. The ants which carried these materials showed no appreciation of leverage or sense of balance. An ant would often be seen carrying a twig, say, an inch long, by one end, thus subjecting its jaws to the effect of considerably more stress than necessary. It might struggle along in this fashion, climbing some obstacles only with great difficulty, but never changing its cumbersome hold on its burden.

X. Discussion

In the preceding sections (V-IX) the connecting thread seeming to run through the aspects of the biology described is the lack of specialization and fine coordination in the colony.

Unfortunately there appears to be little mention in the literature of the features described so their uniqueness or unusualness (if any) is difficult to evaluate. Only the material used for capping nests appears to have been noticed (Wheeler 1926), several groups being referred to which seem to utilize a variety of materials, as with *I. detectus*.

Although the Dolichoderinae are not regarded as specially primitive, *I. detectus* seems, in much of its observed behaviour, to display little specialization. Perhaps if this statement can be regarded as even approximately valid, it helps to explain the wide geographic distribution of the species.

XI. Orientation

The orientation of *I. detectus,* leaving and returning to the nest along trails, is difficult to reverse. An ant oriented towards or away from the nest tends to keep moving in that direction until it reaches the nest or completes a foraging expedition. Several experiments served to illustrate the tendency to preserve this "inward-moving" or "outward-moving" orientation.

The method employed was to reverse the direction of travel by means of a piece of stiff, folded notepaper. The notepaper was brought down in front of an advancing ant, wall-like, and moved along the ground towards it. Actual contact with the ant was generally unnecessary to turn it and make it move in the reverse direction.

When an ant had been turned, it usually turned back again with a smooth looping movement, to face its original direction. Each ant was therefore turned three times and then left to find its own final course. Its orientation was deemed to have been successfully reversed if, after the third reversal, its reverse of orientation was permanent.

All experiments were carried out about 20 yd. from nest I in trail 1, this being the most suitable site. The results are given in Table 2.

Table 2
REVERSAL OF ORIENTATION

Date	No. Attempted to Reverse		No. Successfully Reversed	
	Outgoing	Incoming	Outgoing	Incoming
15.i.51	20	23	10	4
18.ii.51	1	8	1	1
24.ii.51	10	15	3	5
1.iii.51	7	6	6	0

This shows that orientation was difficult to reverse, only 33 per cent. of the total number tested being reversed successfully. The incoming ants were relatively harder to reverse (19 per cent.) than the outgoing (53 per cent.).

On Febuary 24 and March 1 the smooth looping curve mentioned above had disappeared as a response to reversal. It was replaced by an erratic, uneven type of reorientation curve, wholly unlike the former. The significance of this change is not understood.

It was decided that the criterion of success in reversing orientation should be that the ant proceed for at least 5 yd. in a direction the reverse of its original one. A variable time was needed for ants to decide upon their final courses after their original ones had been disturbed. In their initial retreat before the moving obstruction ants would often become dishevelled and dusty, needing time to readjust themselves.

XII. Smell and Sight as Bases for Orientation

As it is generally accepted that ants orient themselves by means of some form of "odour trail" (MacGregor 1947; Wheeler 1926, p. 532) experiments were carried out to see if this was so for *I. detectus.*

Bonnet's experiment (see MacGregor 1947) of drawing a finger across the trail in front of an incoming forager was tried, but no effect was seen on the ability of ants to cross this erased section while maintaining their previous orientation. As it was thought the ants might be tracing the trail around the edges of the erased section, the dimensions of this strip were gradually increased until it was about 1 yd. wide (across the trail) and the same length (along the trail), and about an inch below the surrounding soil.

Most ants were still able to cross this strip. Some, however, displayed confusion. For these, a successful crossing was probably the result of their continuing in a fairly straight line across the strip, there being no stimuli to turn one way or the other. Confusion was possibly mostly the result of the unfamiliar texture of the heavily erased strip.

Antennae were removed from incoming foragers, which were then replaced on the trail. Some moved in a homeward direction, which could have been chance. Some seemed confused; their ability to follow the trail may have been removed, or perhaps they were merely suffering from nervous disorganization following a major loss of sensory equipment.

It is interesting that following heavy rain, which would presumably wash away odour trails, the first foragers to leave the nest had no difficulty in following usual main trails or in retracing them back to the nest.

While it is well known that another kind of orientation is claimed for ants (Santschi 1911; Brun 1914)*, namely that of a "light-compass reaction", it is difficult to see how such a reaction could apply to *I. detectus* because the trails were often not straight, were sometimes shaded in parts, and the ants were unaffected on dull days, when scattering of the Sun's rays occurred.

Perhaps MacGregor's (1947) idea that ants employ several senses in deciding the correct path is correct; some of the senses serving alone on occasion, but under normal conditions complementing each other. If such be the case, memory (Wheeler 1926, p. 533) must also assist foraging and homing.

XIII. Territoriality

Elton (1932) reported territoriality among wood ants (*Formica rufa*). He noted that different nests of the same species, though obviously situated close to each other, had territory, and trails leading to trees, which did not encroach upon those of other nests.

Like Elton's ants, *I. detectus,* in the main, manifested territoriality. The trails from each nest tended not to encroach upon the trails or territories of others. Many trails ended in trees. The few important exceptions—referred to henceforth as "common trails"—will be dealt with later. The trails of the main nests studied are shown in Figure 4.

* Quoted by Fraenkel and Gunn (1940).

As confirmation of this general appearance of territoriality, it was decided to follow Lubbock's (1888) example and find out whether ants of a particular nest attacked ants of the same species from a different nest. On March 23 ants from nest III were placed on nest IV and vice versa. Similarly, on March 23 and 25, ants from nest V and II were placed on nest III. Controls were used also, being picked up, held for a short time, and then placed on the nest because it was thought that an odour from human fingers could cause ants to attack those from other nests which had been handled. The results are collected in Table 3.

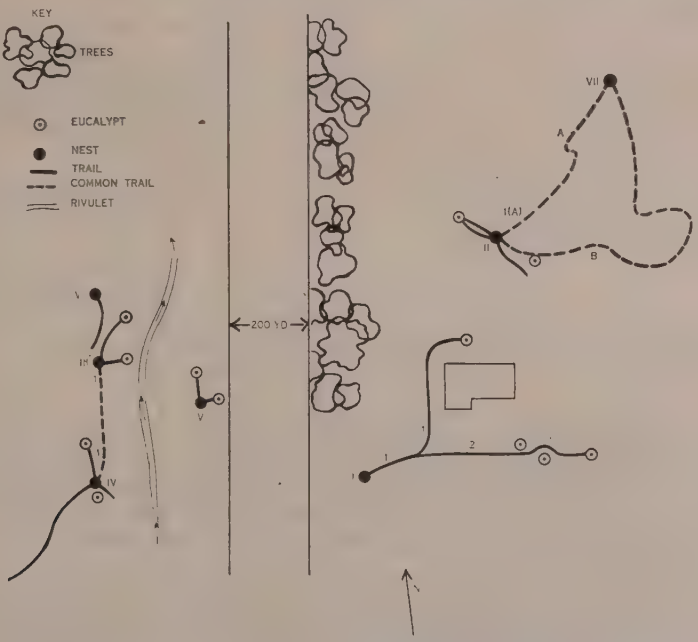

Fig. 4.—Nests and trails employed in this study, and their relationship to one another.

Thus it is seen that of 20 ants tested, 70 per cent. were rejected. No controls were rejected. This supports the idea that nests are units, complete in themselves, with independent lives. The term "rejected," as used above, indicates that an ant was seized or attacked and held, and could have culminated in the victim being dragged into the nest. It is distinct from acceptance, where even though an ant might have been examined cautiously, caused excitement, or even held momentarily, the interest created was only of a passing nature, ultimately harmless to the ant being tested.

When an ant placed on a nest other than its own was being examined by the inhabitants of that nest, it was subjected to an interesting treatment. This consisted in more or less sudden darts at the stranger from all directions, culmi-

nating in touching it with the antennae. The darting movements were quick, and the contacts varied from light to quite rough. The stranger ant almost always behaved in a manner similar to that to be described in the next section.

TABLE 3
REJECTION OF STRANGER ANTS

No. Taken	Rejects	Controls	Rejects	Remarks
23.iii.1951, from III to IV:				
5	4	5	0	One control caused excitement and activity when replaced
From IV to III:				
5	2	5	0	Two controls caused excitement and activity; one seized momentarily
From V to III:				
5	3	5	0	Three controls caused excitement; two seized momentarily
25.iii.1951, from II to III:				
5	5	5	0	Two controls seized momentarily; two others caused slight excitement

XIV. COMMON TRAILS

The common trails—only three were noted—are almost the antithesis of territoriality. That between nests III and IV was the one most studied. Early in the day (about 7 a.m.) ants would leave nests III and IV along this trail (1—1), those from nest III heading towards IV and vice versa.

These excursions resulted in a series of little groups or aggregations all along the common trail, consisting of three or four up to, say, 20 ants. They were generally circular in disposition, with the heads of the ants more often towards the centre of the circle than towards the periphery, but the shape was plastic, varying from group to group and with time. The bodies of the ants were raised off the ground, on legs more extended than usual (a position best described by saying that they appeared to be on "tip-toe"). Their abdomens were raised still higher, above the level of their already elevated thoraces. The movements of those assuming this position were jerky and sudden, without the usual coordination. They quivered almost continually. There seemed to be some kind of communion between them, as pairs would touch antennae, and then break apart, sometimes repeating this again and again with each other, and with other ants. This was sometimes followed by fresh and perhaps more noticeable outbreaks of quivering, with almost violently exaggerated movements. The whole behaviour pattern might be continued almost indefinitely, or be merely of a few seconds duration, depending on how long an ant stayed in the aggregation.

There was an active incoming and outgoing traffic along trail 1—1, connected with both nests, despite the aggregations. Sometimes ants from these main streams would join aggregations, sometimes leave them. Notwithstanding this meeting of ants from two nests it was felt that there was probably little actual exchange between nests III and IV.

As can be seen in Table 3, ants from nest III were not particularly welcome in nest IV and vice versa. Further tests were carried out by taking ants at random from the aggregations in the common trail and placing some on nest III, others on nest IV. The results are given in Table 4.

TABLE 4

TREATMENT OF ANTS FROM TRAIL 1—1 BY ANTS OF NESTS III AND IV

Nest No.	No. Placed on Nest	Rejects	Remarks
III	7	3	One of those accepted caused great excitement
IV	7	3	Two of those accepted caused great excitement, other two momentarily seized

Thus although the ants meet in trail 1—1 without quarrelling, it does not seem that their friendliness would extend to the point of actual exchange of nest members.

The common trails between nests II and VII provided a still more interesting picture. Ants were followed down trail 1 (common trail *A*) and common trail *B* from nest II to nest VII, where they were seen to enter the nest. None of the aggregations seen between nests III and IV was observed here. This was a case of free and completely open social intercourse and exchange.

On April 1, four ants were taken from nest II and transferred to nest VII; two went down holes freely, and none was molested. Four ants were transferred from nest VII to nest II; three of them went down holes freely, none was molested. Furthermore, none of the previously described manifestations on meeting enemies was observed.

XV. Discussion

Although territoriality is, in general, maintained among these ants, the interesting exceptions (or partial exceptions) noted provide something of a problem.

The explanation of these exceptions is possibly something along the lines indicated to the author by K. C. McKeown in personal communications. Mr. McKeown has seen what he thinks may be new colonies formed as "offshoots" from an established nest. These branch nests later appear to become independent and separate, presumably by increase in size and organization on their own part, so that they become self-sustaining; or by being compelled to become independent by decline of the parent nest.

If this is correct then one can see that nests II and VII represent a parent and branch nest (it is difficult to say which is the parent) which have not yet completely divided, and nests III and IV may represent a parent and branch nest in which division has gone still further but is not yet fully completed.

During the course of this work sexual forms of this ant have not been seen (alate or dealate).

XVI. Acknowledgment

The author wishes to thank Dr. A. G. Nicholls for a critical reading of the manuscript.

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THE PARAMPHISTOMES (TREMATODA) OF AUSTRALIAN RUMINANTS

II. THE LIFE HISTORY OF *CEYLONOCOTYLE STREPTOCOELIUM* (FISCHOEDER) NASMARK AND OF *PARAMPHISTOMUM ICHIKAWAI* FUKUI

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[*Manuscript received January* 5, 1953]

Summary

A description of the development at 27°C. of *Ceylonocotyle streptocoelium* (Fischoeder 1901) Näsmark 1937, a paramphistome from the rumen and reticulum of sheep and cattle in Australia, is given in detail.

Eggs hatched after 16 days' incubation and miracidia penetrated the intermediate host, a planorbid snail, *Glyptanisus gilberti* Dunker 1848, through the mantle cavity. The development of the larval stages of the parasite within the intermediate host was completed 34 days after infection, when cerariae were secreted by snails.

Cysts of *C. streptocoelium* fed to sheep and cattle showed that flukes reached maturity in the rumen in 48 and 56 days respectively. The life cycle of the fluke, therefore, was completed in a minimum period of approximately 3½ months under these conditions.

It was found that temperature had a marked effect on the rate of development of larval stages within the molluscan intermediate host, the developmental period at 20°C. being twice as long as that at 27°C.

The various stages occurring in the molluscan intermediate host are described in detail.

The development of *Paramphistomum ichikawai* Fukui 1922 is compared with that of *C. streptocoelium*. The rate of development was found to be more rapid than for *C. streptocoelium* under the same conditions. Eggs hatched after 12 days incubation and cercariae were secreted from the intermediate host, *Segnitilia alphena* Iredale 1943, 25 days after infection.

Flukes were found to reach maturity in sheep 49-51 days after cysts had been fed. The eggs and intra-molluscan stages are similar in both species, but the cercariae may be readily distinguished by anatomical differences in their excretory systems. The life cycle in this species takes approximately 3 months to complete under these conditions.

The molluscan intermediate hosts of the two species of amphistomes are described and notes on their bionomics are given.

I. Introduction

Although the gastro-intestinal parasites of Australian cattle and sheep have received a large measure of attention from various workers in recent years, the species of Paramphistomidae in the rumen and reticulum of these hosts have been virtually neglected. Reports by Roberts (1934), Ross and Gordon (1936),

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and Edgar (1938) have indicated that the immature forms in the small intestine can be seriously pathogenic, and that the adult forms in the rumen and reticulum were considered to be *Paramphistomum cervi* (Schrank 1790) and *Cotylophoron cotylophorum* (Fischoeder 1901).

A preliminary report by the author (Durie 1949) on the life history of these amphistomes implicated the snails *Glyptanisus gilberti* (Dunker 1848) and *Segnitilia alphena* (Iredale 1943) as the intermediate hosts of *P. cervi* and *C. cotylophorum* respectively. Taxonomic studies (Durie 1951) later showed that neither of these species was present in Australia and that the species previously referred to under these names were *Calicophoron calicophorum* (Fischoeder 1901) Näsmark 1937, *Ceylonocotyle streptocoelium* (Fischoeder 1901) Näsmark 1937, and *Paramphistomum ichikawai* Fukui 1922. *G. gilberti* was the intermediate host of *C. streptocoelium* and *S. alphena* the intermediate host of *P. ichikawai*. The snail vector of *C. calicophorum* has not yet been determined. Detailed life history studies on these two species of amphistomes were then commenced and are reported here.

Several workers in overseas countries have reported life history studies on various species of amphistomes. Looss (1896) worked in Egypt with *P. cervi*, Porter (1921) and Grobbelaar (1922) in South Africa with *C. calicophorum*, Bennett (1936) in the United States with *C. cotylophorum*, a species since reidentified by Price and McIntosh (1944) as *P. microbothrioides*, Scrivasta (1944) and Sinha (1950) in India with *P. explanatum* and *C. cotylophorum* respectively, and Jonathan (1950) in New Zealand with an undetermined species, later identified by the author as *C. calicophorum*. The descriptions of the life histories of these species indicate that amphistomes follow a general plan of development in which only one molluscan intermediate host is involved and the cercariae are liberated from the rediae into the host tissues while still in an immature state and complete their development subsequently while free in the tissues of the snail host. Infection of the final host occurs by the ingestion of herbage on which the cercariae have encysted. The species described here follow a similar plan of development.

II. The Life History of Ceylonocotyle Streptocoelium (Fischoeder 1901) Nasmark 1937

(*a*) *Materials and Methods*

Adult specimens of *C. streptocoelium* were obtained from the rumen and reticulum of cattle slaughtered at an abattoir near Brisbane. Flukes were identified initially from stained sections but later it was found possible to identify living flukes by microscopical examination of whole specimens, using the shape and appearance of the testes and the appearance of the genital atrium. Specimens were removed from a freshly opened rumen by means of forceps and placed in Tyrode physiological saline solution. After examination for identification they were transferred to petri dishes containing the same medium and incubated in the darkness at 37°C.

Under these conditions large numbers of eggs were deposited during the first 3 days and flukes lived for approximately 5 days, providing that the Tyrode solution was changed daily. Jonathan (1950) found it possible to maintain a culture of living flukes for 30 days in this solution at 35°C. The eggs were collected and washed in several changes of distilled water and were incubated in distilled water at 27°C. The water was changed daily throughout the developmental period to minimize infection by a parasitic chytridiacean fungus.

Mass hatching of eggs containing fully developed miracidia occurred when the eggs were exposed to sunlight, large numbers of miracidia being present in the culture 16-20 min. after removal from the incubator.

Snails used for infection trials were laboratory-bred specimens of *G. gilberti*. They were exposed to large numbers of miracidia in aquaria in which the temperature was thermostatically controlled at 27°C., and were fed at first on boiled lettuce leaves and later on an artificial snail food reported by Standen (1951). Both foods were highly satisfactory and snail growth was good. When well-developed cercariae were observed, infected snails were isolated in 6 by 1 in. tubes for the collection of metacercariae.

The examination of larval stages was made entirely on living material with the aid of the phase-contrast microscope and vital stains, and a constant temperature of 27°C. was maintained to determine the developmental rate of all free-living and intra-molluscan stages.

(*b*) *Development of the Free-living Stages*

(*i*) *The Egg*

(1) *Description.*—The egg is comparable in shape with that of other members of the Paramphistomidae, being oval in shape with a slight attenuation towards the anterior end. An operculum is present which measures 33 μ in diameter and 2 μ in thickness. It is attached to the shell in the usual manner by interlocking projections which are held together by some kind of cementing substance, as shown by their method of hatching. The shell is unmarked except for a slight projection placed asymmetrically at the posterior end, similar to that reported in the majority of the ova of the Paramphistomidae (Bennett 1936). The egg measures 145-154 μ in length by 70-78 μ in width, the average measurement being 148 μ long by 74 μ wide. It is whitish to transparent in colour and when deposited has about 50 yolk cells, each of which is spherical in shape and contains yellow to green granules. The egg of *C. streptocoelium* is almost indistinguishable from that of *P. ichikawai* except for small differences in size.

(2) *Development.*—When deposited, eggs of *C. streptocoelium* are in an early stage of segmentation, the majority being in the four-cell stage, but some contain as many as eight cells. The ovum is situated slightly posterior to the centre of the egg and is rather indistinct in outline as it is entirely surrounded by yolk cells. It may, however, be distinguished from the yolk cells by its rather more dense appearance and by the absence of granules. Little change takes place in the appearance of the embryo during the first 3 days except that it

increases slightly in size and cell division is rapid. Embryos now average 31.5 μ in diameter and resemble a ball of closely packed cells.

At the end of 5 days the embryo loses its ball-like appearance and becomes elongated along the long axis of the egg (Fig. 1*a*). The divisions between the cells are no longer visible and the embryo increases markedly in size, averaging 55 μ long by 40 μ wide. During this period of rapid growth the yolk material decreases considerably so that the embryo is clearly visible within the yolk mass.

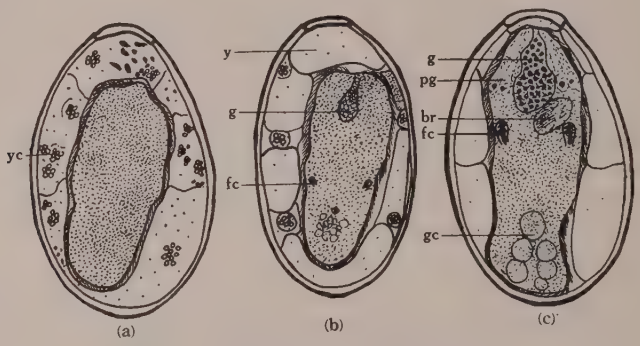


Fig. 1.—*Ceylonocotyle streptocoelium.*

(*a*) Egg at the end of 5 days' development at 27°C. (× 300); *yc,* yolk cells.

(*b*) Egg at the end of 8 days' development at 27°C. (× 300); *fc,* flame cell; *g,* gut; *y,* yolk plug. These and later figures were made with the aid of a camera lucida.

(*c*) Egg at the end of 12 days' development at 27°C. (× 300); *br,* brain; *fc,* flame cell; *g,* gut; *gc,* germ cell; *pg,* penetration gland.

During the 5-8-day period there is an appreciable increase in size, and the cilia and presumably the epidermal plates are developed during the early part of this period. Flame cells and the cells of the primitive gut appear next, but no ducts of the excretory system can be seen. The embryos are clearly visible within the egg, and at the end of 8 days average 68 by 44 μ (Fig. 1 (*b*)). The majority of embryos at this time are quiescent but some may move slightly. It seems evident that the longitudinal and circular musculature must be in an advanced stage of development at the end of 8 days. The yolk cells have for the most part disappeared. Those remaining have lost their cell boundaries and have coalesced into a single yolk mass contained in an envelope surrounding the embryo. At this stage the yolk plug can be observed behind the operculum.

The most noticeable change during the next 4 days is the rapid increase in the size of the embryos, which now have a high degree of motility. Flame cells are conspicuous, and the gut appears fully developed. During this period penetration glands and germ cells can be seen, together with nerve cells. At the end of 12 days embryos average 105 μ in length by 41 μ in width (Fig. 1 (c)).

The apical papilla is fully developed and the yolk plug appears to be in various stages of destruction; some embryos have almost destroyed the yolk plug completely. Cilia may move, but only occasionally and feebly. Apart from the lack of movement in the cilia, the miracidium appears fully developed at the end of 12 days.

Little noticeable structural change occurs during the 12th to 16th day but motility increases to a marked degree and embryos are frequently curled within the egg to accommodate their increased length. Cilia may be seen to beat frequently during the latter part of this period and in most specimens destruction of the yolk plug is complete. Mass hatching of the miracidia occurred after 16 days, i.e. on the 17th day after incubation.

(3) *Hatching.*—Miracidia become very active about 48 hr. before rupture of the operculum, when they attack the yolk plug vigorously by contracting the circular muscles and applying pressure to its posterior surface. The point of application of the apical papilla is changed frequently and at times the miracidium appears to brush the yolk plug with the cilia of the first series of epidermal cells. The time taken to clear the yolk plug from the opercular end of the egg varied and was impossible to determine accurately but usually the plug had disappeared 48 hr. after the miracidium's first attack. During the period of yolk plug destruction movement is confined mainly to the cilia of the anterior portion of the body, which beat feebly and for only a few seconds at a time. The yolk material is now confined in two or three large cells surrounded by an elastic membrane usually situated on one side of the miracidium. About 30-60 min. before the egg hatches the cilia commence to beat rapidly, and at the same time vigorous elongation and contraction of the body takes place. This period of activity may only last for several minutes, after which the miracidium again becomes quiescent for a short period. After a period of rest, usually longer than the period of activity, the process is repeated. Finally, cilial action becomes more vigorous and the envelope containing the yolk material is ruptured. The miracidium is now stimulated to even greater activity and the apical papilla is applied to the operculum with renewed vigour.

It is thought that, when the membrane surrounding the yolk ruptures, the apical papilla can then be placed in direct contact with the actual junction of the operculum and the shell. The miracidium may apply the apical papilla strongly for several moments, at the same time rotating it as though contacting the whole junction of the operculum with the shell.

At this stage, some miracidia turn completely round in the egg and return to the operculum again. Shortly after the application of the apical papilla to the opercular junction, a transparent fluid appears in the vicinity of the apical papilla and is spread by movements of the papilla over the junction. Almost immediately afterwards the operculum opens, usually without any further muscular action, and the miracidium is released from the egg by muscular contraction and cilial action. The escape of the miracidium from the egg is usually completed within a period of several seconds to 2 min.

(ii) *The Miracidium*

(1) *Description.*—The miracidium of *C. streptocoelium* (Fig. 2) agrees closely in structure with that of *P. microbothrioides* as described by Bennett (1936). Miracidia are barely visible to the naked eye but their presence is quite apparent when large numbers are involved, as when the eggs in a culture hatch simultaneously. The body shape is variable, being quite flexible and subject to considerable change, but when swimming freely the shape is pyriform, being broadest just posterior to the base of the first set of epidermal plates. The body is rounded anteriorly with the apical papilla placed centrally at the tip. Posteriorly the body tapers gradually to a rounded extremity at the posterior end.

Epidermal plates.—The body is almost completely enclosed within a series of ciliated epidermal plates or cells. These conform to the formula given for the Paramphistomidae by Bennett (1936), namely, 6,8,4,2. The first series (anterior) consists of six cells somewhat triangular in shape with the nucleus situated on the posterior margin of each cell. The epidermal cell nuclei show up quite clearly when stained with methylene blue. The series terminates at the widest portion of the body in a position which may be termed the "shoulders" of the miracidium. This series is covered with cilia which gradually increase in length towards the posterior end and move in a similar manner to the other cilia on the body.

The eight cells of the second series are rectangular in shape with the nuclei situated at the posterior ends of the cells. They extend posteriorly to just behind the middle of the body and their anterior margin adjoins the posterior edges of the first series. The nuclei of these cells are variable in shape and appear somewhat in the form of a cross, with sometimes more than four arms. The external surface is completely covered with cilia of uniform length.

The four cells of the third series are rectangular in shape, but are narrower at the posterior end due to the tapering form of the miracidium. The nuclei of these cells are similar to those of the first series and are somewhat banana-shaped.

The fourth series consists of two cells which are triangular in shape and have their nuclei situated at the anterior margin. The nuclei are similar in shape to those of series 1 and 3, but are much larger.

The divisions between the plates of each series are difficult to determine in living specimens and the number of cells observed depends mainly on counts of nuclei. However, the divisions are clearly noticeable in optical sections.

The cilia covering the posterior portion of the body are uniform in length and are arranged in longitudinal rows. The lines formed by the basal granules of the cilia are highly conspicuous.

Subepithelial muscles.—The musculature is well developed, as evidenced by the vigorous contractions and extensions of the miracidium. The muscle layers are situated between the subepithelium and epidermal plates, the circular muscle layer being placed externally to the longitudinal muscles.

Primitive gut and associated glands.—The so-called primitive gut is well developed and appears as a pear-shaped structure extending to about one-

quarter the length of the body. The gut is filled with granular particles which move freely within its interior when elongation and contraction of the miracidium occurs. Although the narrow anterior constriction of the gut could be traced to the anterior part of the apical papilla, no opening to the exterior could be seen.

Various workers (Thomas 1883; Sinitsin 1931) regard this structure as a primitive or vestigial gut, whereas others consider it to be glandular in nature (Price 1931; Lynch 1932; Bennett 1936), because of its disappearance on entry into the snail intermediate host. The latter suggestion appears to be the most feasible one since no opening to the exterior can be seen and the life of the miracidium is so short that feeding is unnecessary.

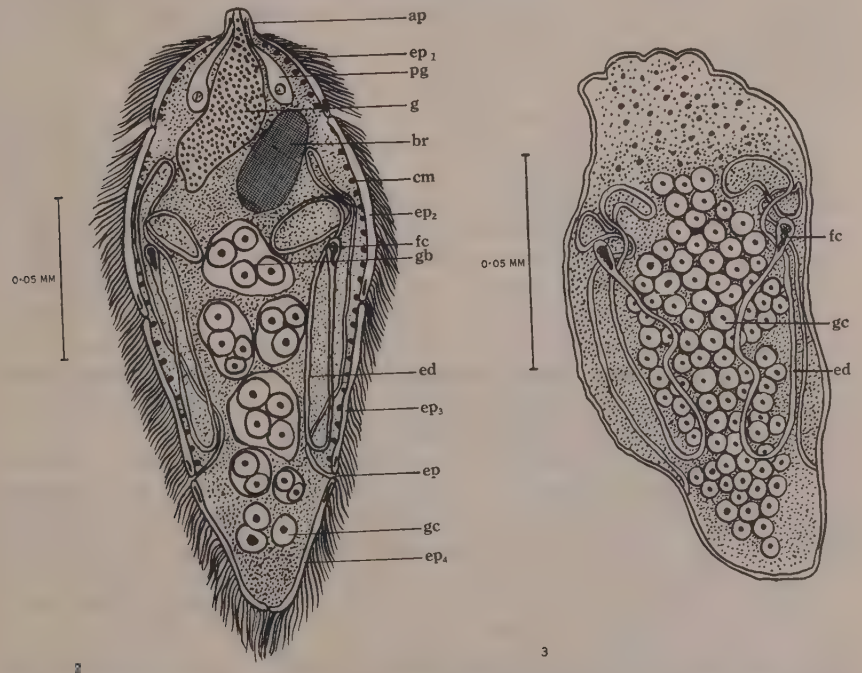


Fig. 2.—*Ceylonocotyle streptocoelium*. Mature miracidium flattened to show internal structure; *ap*, apical papilla; *br*, brain; *cm*, circular muscle band; *ed*, excretory duct; *ep*, excretory pore; ep_1, epidermal plates, series No. 1; ep_2, epidermal plates, series No. 2; ep_3, epidermal plates, series No. 3; ep_4, epidermal plates, series No. 4; *fc*, flame cell; *g*, gut; *gb*, germ ball; *gc*, germ cell; *pg*, penetration gland.

Fig. 3.—*Ceylonocotyle streptocoelium*. Sporocyst after 3 days' development at 27°C.; *fc*, flame cell; *ed*, excretory duct; *gc*, germ cell.

Also in close association with the primitive gut are two pairs of penetration glands, rather difficult to detect, but provided with large, well-defined nuclei at their bases. These glands may play some part in the secretion of fluid responsible for the hatching of the miracidium.

A brain mass is present but no nerves passing from it were observed, although two rather large fibres, somewhat sac-like in appearance, were seen attached to the sensory papillae situated between the first and second sets of epidermal plates.

Germ cells.—These are located in the posterior two-thirds of the body. They can be made readily visible with vital stains and appear as balls of cells enclosed in a membrane anteriorly and as single cells posteriorly.

Excretory system.—This is similar to that described for other miracidia and consists of a single pair of flame cells located laterally below the gut and embedded in a protrusion of the subepithelium. Each flame cell leads into an excretory duct which passes backwards to just above the level of the excretory pore and then loops forwards as far as the flame cell and back again posteriorly to the excretory pore situated between the third and fourth sets of epidermal plates.

(2) *Behaviour.*—The miracidium hatches readily when exposed to light after removal from a darkened incubator, the majority hatching within 20 min. Eggs containing fully developed miracidia may be prevented from hatching by excluding light but the delaying affect of darkness is limited and hatching cannot be delayed for more than 24 hr. Miracidia are positively phototropic. When killed in the extended condition in a solution of "Carbowax" 5000 miracidia measure 203-300 μ (10 specimens), which is considered to be approximately the length of living specimens.

Free-swimming miracidia are very active and swim in straight lines with the body rotating in a clockwise direction. If the miracidium contacts a solid object it will assume a spherical form, flex the anterior end of the body to one side, and swim round to clear the obstruction.

As in most other miracidia (Thomas 1883; Bennett 1936) the length of the free-swimming life at room temperatures is approximately 8 hr. Miracidia move in slow circles towards the end of this time and gradually become more feeble and sink to the bottom, where rapid degeneration of the epidermal cells occurs.

They are stimulated to greater activity when in the vicinity of snails, irrespective of whether the snails present are the correct intermediate hosts or not. This behaviour is characterized by swimming in rapid circles or spirals in the vicinity of the snail, and at times applying the apical papilla to the protruding soft parts, the head, tentacles, or foot. If, however, the snail present is not the normal intermediate host, death of the miracidium occurs very rapidly, the snail leaving a trail of dead or dying miracidia in its path. On the other hand, when the normal intermediate host is available, miracidia can be observed swimming actively even after 4-5 hr. contact with the snail.

(3) *Penetration of Miracidium into Snail.*—Observations on the penetration of the miracidium into the snail host were confined to young snails in which the transparency of the shell and mantle tissues facilitated close observation of the process of penetration. Miracidia were never observed to penetrate the exposed soft parts of the host, such as the head, tentacles, foot, etc., as reported

by Bennett (1936) for *P. microbothrioides*, but infection was always effected by way of the pneumonostome or pulmonary aperture and through the posterior wall of the mantle cavity.

Infection trials carried out with snails of varying ages showed that young snails are more susceptible to infection than older ones. In young snails the mantle cavity is completely filled with water and the pneumonostome is permanently open, water being circulated in the mantle cavity by cilial action. In older snails, on the other hand, the mantle cavity is either wholly or partially filled with air, and the pneumonostome is opened only when the snail is actively expelling and replacing air at the water surface. Entry by miracidia into young snails by this route would therefore be unobstructed and progression within the mantle cavity facilitated.

After entering the mantle cavity the miracidium almost immediately attaches itself to the posterior end adjacent to the heart cavity. Some miracidia may release themselves and swim out of the mantle cavity, but in the majority penetration continues. The apical papilla is extended and pressed closely to the wall of the mantle cavity accompanied by rapid movements of the cilia. In several minutes the apical papilla has entered the wall and the miracidium makes strong muscular contractions as though forcing the apical papilla further forward. The cilia now beat more slowly and further penetration of the miracidium is effected almost wholly by muscular movement. This is slow until the miracidium has penetrated to the level of its third set of epidermal plates, when it becomes rapid and the whole remaining body portion enters the wall in a second or less. Complete penetration took approximately 30 min.

After penetration of the mantle wall, miracidia were observed in the heart cavity and in some specimens movements of the cilia could still be seen. It was not possible to detect whether any secretion was produced by the miracidium during penetration. The ciliated epithelial plates are shed 2½ hr. after penetration into the heart cavity. The cilia are lost from the posterior end first and those of the first set of epidermal plates are shed last. The larva is extremely active but the internal structures show no marked changes from those of the free-swimming miracidium.

(*c*) *Development in the Intermediate Host*

(i) *The Sporocyst*

Twelve hours after penetration the ciliated epidermal plates of the sporocyst have been completely shed, no traces of any cilia are visible, and the primitive gut and brain have either wholly or partially degenerated. The excretory system is unchanged and, if anything, is more clearly visible than in the miracidium. The sporocyst is now elongate but highly contractile, and at times may be almost spherical, changing its shape continuously. The anterior end no longer retains the rigidity seen in this part of the miracidium but is variable in shape and appears knobbled at times. This appearance is characteristic of the anterior end of this stage in development throughout the major portion of its existence. Sporocysts at this stage average 93 by 53 μ.

There was no further change in the internal structure of the sporocyst until the third day, apart from a slight increase in size and a clearer definition of the germ cells, which have been reduced from the germ balls of the miracidium to single cells (Fig. 3).

By the fifth day of infection the sporocyst tends to become ovoid in shape, although it is still active and occasionally makes attenuating movements. The anterior end is typically crinkled in appearance and the flame cells have become larger with conspicuous excretory ducts. The reproductive cells have commenced to form into definite groups or balls six to eight in number.

During the 5-8-day period of development the sporocyst increases markedly in size and shows rapid formation of a redia, invariably the most anterior specimen. The most highly developed redia possesses a pharynx, a gut, three pairs of flame cells, and primoidal germ balls (Plate 1, Fig. 1). The flame cells of the sporocyst have reached their maximum size and the excretory ducts are large and less convoluted.

After 11 days, both sporocysts and small rediae were found in the tissues of the snail, situated mainly on the anterior edge of the liver tissue. Sporocysts reach their maximum size at this time and are fully mature. No visible structures except flame cells and excretory ducts, which have become almost direct channels without convolutions, are apparent. Living sporocysts show the body wall to be thickened at the extremities. The circular muscle bands are clearly visible but the longitudinal muscle bands could not be detected.

Sporocysts in varying stages of development were present at this time and it is evident that all sporocysts do not develop at a uniform rate. The maximum number of rediae observed within a single sporocyst was eight; other specimens contained from two to six rediae. Rediae were not observed in the process of liberation from the sporocyst but the presence of sporocysts with flared or torn anterior ends, closed off from the rest of the body by a constriction, supports the conclusion that they are liberated in the manner described by Bennett (1936), i.e. by rupture of the anterior body wall.

(ii) *The Redia*

(1) *Description.*—The primoidal germ balls of the redia appear early in the development of the sporocyst, and the internal structures are for the most part fully developed when the redia is liberated from the sporocyst. However, at this stage no birth pore is evident.

Digestive system.—This is formed in a manner similar to that described by Bennett (1936) for *P. microbothrioides.* A central mass of cells whose nuclei measure 8-9 μ in diameter becomes divided in the centre to form the lumen of the gut, while anteriorly another similar concentration of cells forms the pharynx. These two structures later become connected by an oesophagus. Some rediae were found to have the digestive tract well developed 8 days after infection.

Rediae measuring 140 by 70 μ have a well-developed digestive system similar in appearance to that seen in liberated rediae with the gut extending well posterior to the middle of the body. In a redia which measured 207 by 82 μ the pharynx measured 27 by 40 μ in width, the oesophagus 30 μ in length, and the

gut 100 by 50 μ. The gut extended to four-fifths of the length of the body. A plug occluding the anterior portion of the pharynx, as described by Bennett (1936), was also present.

Excretory system.—The excretory system of the redia consists of three pairs of flame cells measuring 8-9 μ long by 3 μ in width. They are situated at the anterior end, middle, and posterior end of the body, and are connected by ducts which open to the exterior on either side of the body from a small vesicle or bladder.

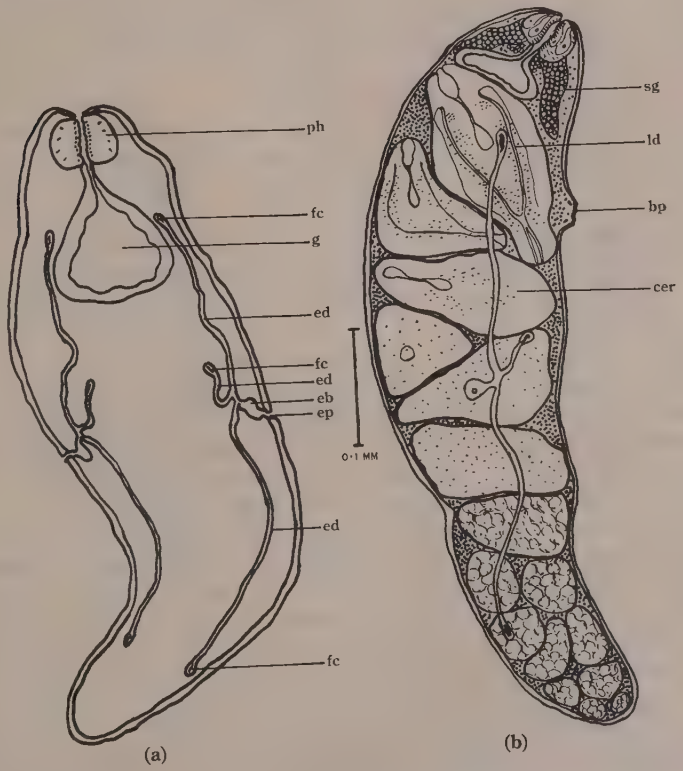


Fig. 4.—*Ceylonocotyle streptocoelium.* (*a*) Mature redia showing structure of excretory system (dorsal view); *eb,* excretory bladder; *ed,* excretory duct; *ep,* excretory pore; *fc,* flame cell; *g,* gut; *ph,* pharynx. (*b*) Mature redia showing birth pore and developing cercariae (lateral view); *bp,* birth pore; *cer,* cercaria; *ld,* main lateral excretory duct; *sg,* salivary glands.

The anterior pair of flame cells is situated laterally to the gut. A duct passes posteriorly from each to about the middle of the body where it unites with a duct from the middle pair of flame cells and with a duct running anteriorly from the posterior pair of flame cells. The common duct expands to

form a bladder which opens to the exterior by an excretory pore situated laterally about two-thirds the length of the body from the anterior end (Fig. 4 (*a*)).

Nerve cells.—A group of cells 10-12 μ in diameter containing nuclei 6 μ in diameter surrounds the oesophagus; they are thought to be nerve cells. These cells are similarly situated to those described by Bennett (1936) for *P. microbothrioides*. No nerve fibres were seen running from the area.

Salivary glands.—In the mature redia these consist of a paired structure lying beside the oesophagus. Each gland consists of a large number of cells surrounded by a thin membrane extending from the pharynx to the anterior portion of the gut. Also associated with the pharynx are eight large cells believed to be glandular in function.

(2) *The Free Redia.*—Rediae were found free in the tissues of the snail 10-11 days after infection and measured 200-300 μ in length by 90-100 μ in width. Prior to their liberation fully developed rediae within the sporocyst measured 200-220 by 70-90 μ, the gut 40-50 μ in diameter, pharynx 28-30 μ in diameter, and the oesophagus 30-35 μ in length.

Rediae are variable in size when liberated from the sporocyst and it is evident that liberation does not depend on the redia attaining a certain size, but more likely on the degree of development and activity attained within the sporocyst (Bennett 1936).

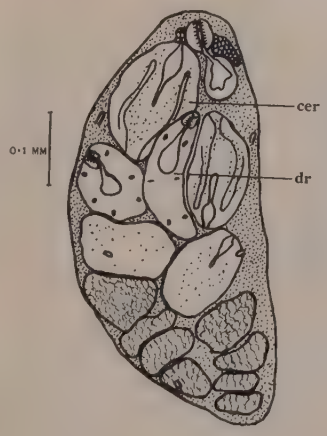
Birth pore.—This develops in rediae after liberation from the sporocyst and is seen first in rediae 18 days after infection, measuring 290-300 μ in length. This structure increases in size and becomes more conspicuous as the redia approaches maturity. In the mature redia it is situated on the ventral surface of the body just behind the gut about 170 μ from the anterior end.

After liberation from the sporocyst the redia increases greatly in length, mainly owing to the rapid growth of developing cercariae contained within the body. The gut, which now appears smaller, actually remains the same size throughout development. Rediae attain their maximum size 21 days after infection, just before the liberation of cercariae. They then measure 0.5-0.9 mm. in length and contain 15-30 developing cercariae, of which the anterior ones are the most advanced (Fig. 4 (*b*)).

(3) *Daughter Redia Formation.*—In one group of snails daughter rediae were observed developing within rediae together with cercariae (Fig. 5). Some of these daughter rediae were highly developed 22 days after infection. Only one to three daughter rediae were seen at any one time in the mother redia and their presence did not extend beyond the 24th day after infection, when subsequently only rediae containing cercariae were seen. In seeking an explanation for the production of daughter rediae by this group of snails two possible factors come to mind. Firstly, the temperature of the aquarium in which these snails were maintained dropped from 27 to 20°C. for an unknown period, probably 2 days. The production of daughter rediae may, therefore, have been a temperature or possibly a shock effect. On the other hand, the writer has evidence that snails on a high plane of nutrition and infected with a single miracidium will produce up to seven times the number of cercariae that can

be theoretically expected. An output of such a large number of cercariae can only be explained by the formation of daughter rediae. Thus, in a well-nourished host, daughter rediae may have a normal place in the life cycle of this trematode.

Daughter rediae measured 220 by 80 μ, while in the same mother redia the most advanced cercariae measured 216 by 92 μ. They are readily distinguished from developing cercariae as they appear yellowish in colour when compared with the whitish grey colour of cercariae. They also exhibit much greater activity within the mother redia, actively elongating and contracting, whereas cercariae are relatively passive at this stage. In addition, the daughter rediae have a more highly developed gut, and their three pairs of flame cells are conspicuous.



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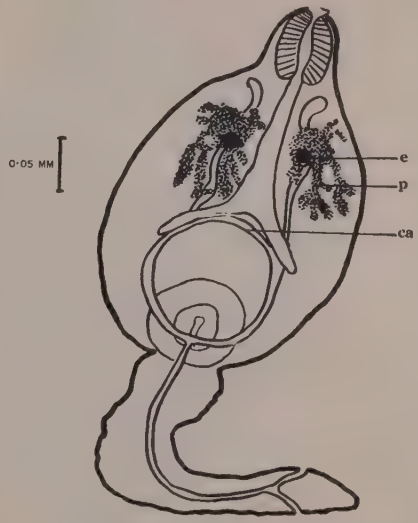

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Fig. 5.—*Ceylonocotyle streptocoelium.* Redia showing development of daughter rediae together with cercariae; *dr,* daughter redia; *cer,* cercaria.

Fig. 6.—*Ceylonocotyle streptocoelium.* Developing cercaria showing pigment spreading in the region of the eyespots; *ca,* cross anastomosis; *e,* eyespot; *p,* pigment.

(iii) *The Cercaria*

(1) *Development.*—As in other amphistomes, the cercaria of *C. streptocoelium* is released in an immature condition and continues its development in the tissues of the snail intermediate host, being ultimately secreted by the snail as a mature cercaria. In the author's experiments at 27°C. cercariae were liberated from rediae 21 days after infection and were secreted by snails 13 days later.

The cercarial germ balls appear early in the development of the redia, and although only few in number are clearly distinguishable from the rest of the body structure when the redia is liberated from the sporocyst. The develop-

ment of the germ balls in the redia is not uniform, being most highly developed in the anterior portion and least developed posteriorly. Little differentiation in structure of the germ ball is seen until it reaches a length of 80 μ, when the cells lose their nucleated appearance and assume the form of a mass rather than of a ball of cells. At this stage the embryo becomes slightly attenuated.

Shortly after this time the primoidea of the digestive and excretory systems appear (Fig. 4 (*b*)). The digestive system appears as two cavities and gives the impression of an hourglass. These cavities later become connected by an oesophagus, the anterior cavity forming the pharynx and the posterior cavity the rhabdocoel intestine. Little further development takes place in this system until after the birth of the cercaria, except that the pharynx becomes differentiated and functional and the rhabdocoel intestine bifurcates, grows laterally, and then posteriorly.

The excretory system appears as two canals situated on either side of the mid line of the cercaria, opening separately at the posterior end of the body. When the cercaria reaches approximately 100 μ in length the tail is constricted off from the posterior end of the body and appears as a rounded projection. Later in the development of the excretory system another lateral canal, evidently a continuation of the main lateral canals at the anterior end, can be seen running parallel to the latter towards the posterior end of the body. This canal becomes conspicuous owing to the fact that it contains a flagellum which beats along its whole length from the posterior end to the junction with the main lateral excretory duct. This duct retains its flagellum in the mature cercaria. No flame cells could be seen.

The lateral excretory ducts fuse in the vicinity of the junction of the tail and body and later fusion takes place throughout the length of the tail, but the openings to the exterior remain separate towards the posterior end of the tail. These openings are placed on the dorsal and ventral surface in the mature cercaria and open from a dilated bladder at the posterior portion of the caudal excretory duct. Before birth of the cercaria an excretory bladder and excretory pore are formed. The primoidea of the eyespots are developed before birth and cystogenous cells with conspicuous rods are numerous.

Following birth, the cercaria becomes feebly motile, the eyespots develop rapidly, the tail increases greatly in length, and the body of the cercaria grows rapidly. Pigment is developed round the eyespots a short time after birth and spreads laterally and posteriorly over the dorsal surface of the body, appearing as finger-like projections emanating from the region of the eyespots (Fig. 6). The pigmentation increases until the cercaria reaches maturity, when the body appears pigmented uniformly over the dorsal and lateral surfaces, and to a lesser extent on the ventral surface. The pigment is superficial and does not extend far below the cuticula.

At birth the cercaria possesses a group of cells at the ventral posterior end, which develops to form the acetabulum. As the acetabulum begins to develop, the lateral excretory ducts become united by a cross anastomosis which runs anteriorly and dorsally to the level of the bifurcation of the intestine (Fig. 6).

As development proceeds the cystogenous cells increase greatly in number and in the mature cercaria the whole body appears to consist of these cells with their enclosed rods largely obscuring the internal organs.

(2) *The Mature Cercaria.*—The mature cercaria (Fig. 7) is black to dark brown in colour and possesses two well-marked eyespots. It is highly motile and the body is continually elongating and contracting. At times the anterior portion may be folded back under the ventral surface, giving the body an almost spherical appearance. Elongated cercariae appear somewhat pear-shaped.

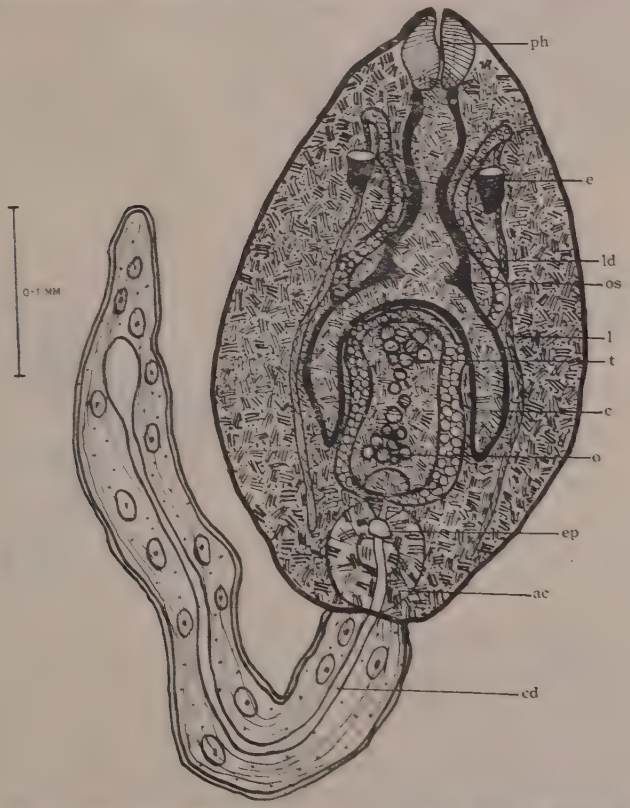


Fig. 7.—*Ceylonocotyle streptocoelium*. Mature cercaria showing the internal structure (dorsal view); *ac*, acetabulum; *c*, caecum; *cd*, caudal excretory duct; *e*, eyespot; *ep*, excretory pore; *l*, lateral duct; *ld*, main lateral excretory duct; *o*, ovary; *os*, oesophageal sphincter; *ph*, pharnyx; *t*, testes.

It was impossible to detect differences in the measurements of cercariae while in the contracted state and to obtain some degree of accuracy in the dimensions it was found more satisfactory to measure them in the extended condition. For this purpose cercariae were fixed in a solution of 30 per cent.

chloral hydrate and the solution warmed at 37°C. for 10 min., when they became fully relaxed. They were then measured in the solution without a coverslip, to prevent distortion due to pressure. The method proved satisfactory and the dimensions of 10 cercariae of *C. streptocoelium* averaged 358 by 200 μ (336-385 by 189-210 μ).

The tail measures 450 μ in length. Cercariae fixed in the contracted position with warm 10 per cent. formalin measure 236 by 234 μ.

The eyespots are conical in shape with a clear lens placed anterodorsally and lateral to the oesophagus immediately behind the pharynx. Although black, they are quite conspicuous against the dark background of the body.

The acetabulum is situated posteroventrally on the body and measures 100 μ in diameter. This structure is not pigmented and appears as a transparent circular organ at the posterior end, ventral to the junction of the tail with the body (Fig. 8).

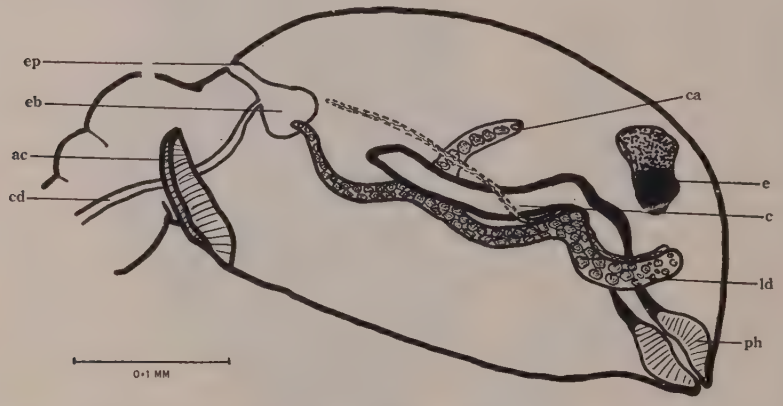


Fig. 8.—*Ceylonocotyle streptocoelium.* Mature cercaria showing relative position of excretory and digestive systems (lateral view, semi-diagrammatic); *ac,* acetabulum; *c,* caecum; *ca,* cross anastomosis; *cd,* main caudal excretory duct; *e,* eyespot; *eb,* excretory bladder; *ep,* excretory pore; *ld,* main lateral excretory duct; *ph,* pharynx.

The internal structures are difficult to trace in the mature cercaria because of the heavy pigmentation of the body and the density of the rather opaque cystogenous cells. However, the major systems may be observed in specimens placed in a solution of "Carbowax" 5000 and flattened by pressure of a coverslip. The "Carbowax" prevents the cercaria from bursting as they do when placed in water.

Digestive system.—The pharynx is a muscular structure measuring 65 by 45 μ which leads into an oesophagus with a moderately developed sphincter at the posterior end where it joins the caeca. The caeca extend on both sides to approximately the posterior third of the body. The digestive system is situated dorsally to the excretory system and its position is illustrated in Figure 8.

Excretory system.—The large lateral ducts of the excretory system are clearly visible and are made conspicuous by the presence of rounded refractile granules. These granules are variable in size and measure from 2 to 12 μ in diameter. The lateral excretory ducts arise from the posterior margin of the bladder and proceed laterally for a short distance before turning upwards and slightly inwards. Near the centre of the body a cross anastomosis is evident and this duct passes between the two lateral ducts, its anterior margins reaching the level of the bifurcation of the caeca. From the junction with the cross anastomosis, the lateral duct continues anteriorly and passes internally to the eyespots until it reaches a point about level with the posterior margin of the pharynx. From this point it turns ventrally and runs back again towards the posterior margin of the body, terminating in the region of the acetabulum (Fig. 7). This part of the duct is rather indistinct and does not contain excretory granules, but shows the presence of the flagellum described previously. Two pairs of flame cells were seen in the region of the pharynx and eyespots, but no pattern was discernible owing to the opacity of the specimens.

The excretory bladder opens to the exterior by the excretory pore situated dorsally in the vicinity of the anterior margin of the acetabulum. A duct runs from the duct joining the bladder to the excretory pore and extends through the major portion of the tail, forming the caudal excretory duct. This duct is expanded at its posterior end to form a small bladder or vesicle from which a dorsal and ventral duct open to the exterior (Fig. 7).

Reproductive system.—The reproductive system is represented only by primoidea consisting of two groups of cells situated posterior to the cross anastomosis of the excretory system and anterior to the excretory bladder. These two groups of cells represent the anterior testes and posterior ovary.

The free-swimming cercaria.—This is clearly visible to the naked eye, especially when viewed against a white background, and swims vigorously upon liberation from the pulmonary aperture of the snail intermediate host.

Cercariae appear to be weakly phototropic and to some extent negatively geotropic, in that encystment most frequently occurs towards the light source and close to the surface of the water. However, these conditions do not always apply and cercariae were found at times encysted on the bottom of the containers in which they had been secreted. If vegetation is present encystment is more rapid and 90 per cent. of the cercariae will encyst on the vegetation in preference to the sides and bottom of containers. The stimulus to encystment on vegetation is probably influenced by light of a definite range of wavelengths reflected by the vegetation. This suggestion is supported by the fact that cercariae would encyst on or near areas marked out by a yellow grease pencil on the outside of the container, but not on areas marked out by a red, green, or blue pencil.

Cercariae are secreted from snails throughout all hours of daylight, but mainly during the morning and particularly between 9.00 and 11.00 a.m. When snails containing mature cercariae are removed from a darkened incubator and exposed to a strong light or to sunlight, cercariae appear within 30

min. It would thus appear that, as mentioned previously, liberation is stimulated to a large extent by the presence of light after a period of darkness.

Liberated cercariae will remain active for from 10 min. to several hours before encysting, the period of free-swimming life apparently depending on the nature of the surfaces available for encystment.

(*d*) *The Metacercaria*

The process of encystment in *C. streptocoelium* is similar to that described by Bennett (1936) for *P. microbothrioides*. The cercaria applies itself to the surface selected for encystment by means of the posterior sucker or acetabulum and the body begins to elongate and contract, and at the same time the anterior portion is moved from side to side. Shortly after settling down, cystogenous material appears around the body of the cercaria and is spread about by means of the motile anterior portion. The tail beats rapidly throughout the whole process and, as the cyst wall appears, the tail becomes less firmly attached to the body. The process of encystment takes about 10 min. and the tail is freed from the cyst wall, apparently by virtue of its own movement, and will continue to swim for several hours after release from the cercaria.

The cyst is rough on the outside but smoothed on the inside by the movement of the cercaria. It is black in colour, darkening with age and measures 225 μ across the base (embryo 155 μ in diameter) and 129 μ high. It will remain viable under optimum conditions for 3 months (Plate 1, Fig. 2).

(*e*) *Effect of Temperature on Development*

The development detailed above was carried out at a constant temperature of 27°C. Another series of developmental rates was carried out at 20°C. and it was found that at this temperature development took almost twice as long as at 27°C. The comparative times for the larval flukes to reach similar stages of development are given in Table 1.

(*f*) *Tissues of the Intermediate Host Invaded by the Larval Stages of* C. streptocoelium

The penetration of miracidia of *C. streptocoelium* in every instance observed was found to take place through the tissues of the mantle cavity of *G. gilberti*. The sporocysts of *C. streptocoelium* are not only motile but actively migrate through the host tissues, and appear to be extremely active at all times. Migration takes place through the heart cavity to the anterior portion of the liver tissue, where the sporocyst usually remains, and in most instances rediae are liberated. Some sporocysts have been found directly below the membrane covering the liver tissue about half way along its length.

The rediae are also active and migrate through and on the surface of the liver tissue towards the posterior end. At this stage of the migration, which takes approximately 10 days from the time of liberation from the sporocyst, rediae are mature and cercariae are ready to be liberated.

Cercariae are liberated in an immature state 21 days after infection and commence to migrate forwards towards the mantle cavity. During this migra-

tion, they increase greatly in size and pigmentation and are finally mature on reaching the anterior edge of the liver, 12 days after liberation from rediae. Mature cercariae make their way to the exterior through the mantle cavity and pulmonary aperture.

TABLE 1

COMPARATIVE DEVELOPMENTAL RATES OF *C. STREPTOCOELIUM* IN THE SNAIL INTERMEDIATE HOST AT 27 AND 20°C.

Stage of Development	Period After Infection	
	At 27°C. (days)	At 20°C. (days)
Mature sporocysts	9	16-20
Free rediae	10-11	20-21
Free cercariae in snail	21	45
Cercaria liberated	34	63

This sequence of larval fluke migration within the snail appears to be the normal one. However, when a heavy infestation is present or when an infection has developed so that larval stages are numerous, little migration sequence can be determined. In heavily infested snails the whole liver tissue and other organs are invaded by rediae and cercariae in all stages of development and later when cercariae approach maturity they may occupy the whole of the internal organs (Plate 2*a*).

Although snails can carry large numbers of *C. streptocoelium* larvae in the later stages of development, a heavy infection with miracidia usually leads to the death of the intermediate host 3-4 days after infection. Should the snail survive the initial period of infection, however, the degree to which the infection develops does not greatly influence the growth of the host, as snails infected when only several days old have reached normal adult size, despite the fact that very heavy infections were being maintained.

Controlled infections of young snails with a single miracidium of *C. streptocoelium* have shown that the ultimate infection attained, as determined by the number of cercariae secreted, depends very largely on the satisfactory growth of the snail host. Snails on a high plane of nutrition secrete many more cercariae than those whose growth has been subnormal during the developmental period of the fluke. It is considered, therefore, that the host-parasite relationship existing in this species is similar to that described by Kendall (1949) in England, for *Fasciola hepatica* and its intermediate host *Lymnaea truncatula,* in which the infection attained in the snail depends on its plane of nutrition during the developmental period of the fluke.

(*g*) *Development in the Final Host*

Cysts of *C. streptocoelium* were fed to sheep and cattle and the time to reach maturity was estimated by examination of faecal samples for the presence of fluke eggs.

Specimens of *C. streptocoelium* were found to reach maturity in 48 days in sheep and 56 days in cattle. The apparent difference between the times to reach maturity in these two hosts may be explained by the greater difficulty in tracing a small number of fluke eggs in the larger bulk of cattle faeces. This prepatent period is much shorter than that recorded for *P. microbothrioides* by Krull (1934) and by Bennett (1936) who give maturity periods of 4 and 3½ months respectively. Bennett considers that *P. microbothrioides* matures at a smaller size in some hosts than in others, an observation based on the findings of Stunkard (1929), who reported that specimens of *P. microbothrioides* reached maturity at a much smaller size in calves than in antelopes. Stunkard's findings were based on the recovery of immature specimens of up to 6 mm. in length from antelopes, while mature specimens from calves were smaller. Whether it is implied that the host influences the maturity period in this species is uncertain. However, trials conducted by the author showed that the prepatent period for *C. streptocoelium* in sheep and calves was approximately similar, namely 48 and 56 days respectively.

The age and size at which this species migrated to the rumen was not determined.

III. Life History of Paramphistomum Ichikawai Fukui 1922

(*a*) *Development of the Free-living Stages*

The methods used in this study of the life history of *P. ichikawai* were similar to those described for *C. streptocoelium*. The development of the larval stages was observed at 27°C.

(i) *The Egg*

The ova of *P. ichikawai* are very similar in appearance to those of *C. streptocoelium* and measure 143 μ long by 64 μ wide (129-148 by 59-67 μ). Although the eggs of this species approach those of *C. streptocoelium* in size, they tend to be narrower. When deposited, segmentation is usually in the four-cell stage and the yolk cells appear similar to those of the eggs of *C. streptocoelium.*

(ii) *The Miracidium*

The miracidium of this species develops more rapidly than that of *C. streptocoelium,* when maintained under similar conditions. Segmentation takes place more rapidly in the early stages of development, and cilia and presumably epidermal cells together with flame cells were seen as early as 4 days after deposition. Some embryos were found to be motile after 5 days and the majority were motile after 6 days' development, when they averaged 108 by 40 μ. The embryo at the end of the 6-day period corresponds closely in size and structural development with that of *C. streptocoelium* after 11-12 days' incubation. After this initial period of rapid development further changes take place at a rate almost identical with that of *C. streptocoelium* and eggs hatch after 12 days' incubation compared to 16 days for *C. streptocoelium.*

Hatching of the egg and release of the miracidium of *P. ichikawai* takes place in a similar manner to that of the previously described species. The miracidia of the two species are structurally identical and approximately equal in size, but those of *P. ichikawai* swim more slowly than those of *C. streptocoelium*. The process of penetration of miracidia into the mantle tissues of its snail intermediate host, *Segnitilia alphena*, and the subsequent loss of ciliated epidermal plates are identical with that described for *C. streptocoelium*.

(*b*) *Development in the Intermediate Host*

(i) *The Sporocyst*

The sporocysts of *P. ichikawai* are similar in structure to those of *C. streptocoelium* but do not show the same degree of activity, and migration does not take place from the tissue of the heart cavity to any great extent. The sporocyst becomes firmly established in what appears to be a small pocket in the tissue of the mantle, and remains in this position until rediae are released. Sporocysts of *P. ichikawai* reach maturity and rediae are first released 8 days after infection in comparison to 11 days for *C. streptocoelium*.

(ii) *The Redia*

Morphologically the redia of this species appears identical with that of *C. streptocoelium*, but development is more rapid and motility occurs more quickly. Rediae of the two species correspond closely in size when released from the sporocyst, and the number produced by each sporocyst also appears to be similar.

(iii) *The Cercaria*

(1) *Description.*—The cercariae of *P. ichikawai* are liberated from rediae through the birth pore in an immature condition 15 days after infection, in comparison to 21 days for *C. streptocoelium*. They are released from snails 25 days after infection, as against 34 days for *C. streptocoelium*. However, the development of internal structures and pigmentation progresses in a manner similar to that described for *C. streptocoelium*.

Although the larval stages of the two species before the formation of the cercariae are almost identical morphologically, and differ only in their rates of development, the cercariae are quite distinct and show well-marked differences in size, structure, and shape (Fig. 9). That of *P. ichikawai* tends to be shorter in comparison to its width than that of *C. streptocoelium*, a difference which is measurable in specimens fixed in warmed 30 per cent. chloral hydrate. The dimensions of 10 specimens treated in a manner similar to those of *C. streptocoelium* average 306 by 207 μ (280-336 by 196-224 μ).

A comparison shows that the cercariae of *P. ichikawai* are on the average approximately 50 μ shorter than those of *C. streptocoelium*, but of equal breadth. This difference in ratio of length to breadth is readily seen when specimens of the two species are flattened between a coverslip and microscope slide (Plate

1, Figs. 3 and 4). The shapes assumed by the specimens, rounded for *P. ichikawai* (Plate 1, Fig. 3) and elongate for *C. streptocoelium* (Plate 1, Fig. 4), are quite characteristic of the two species.

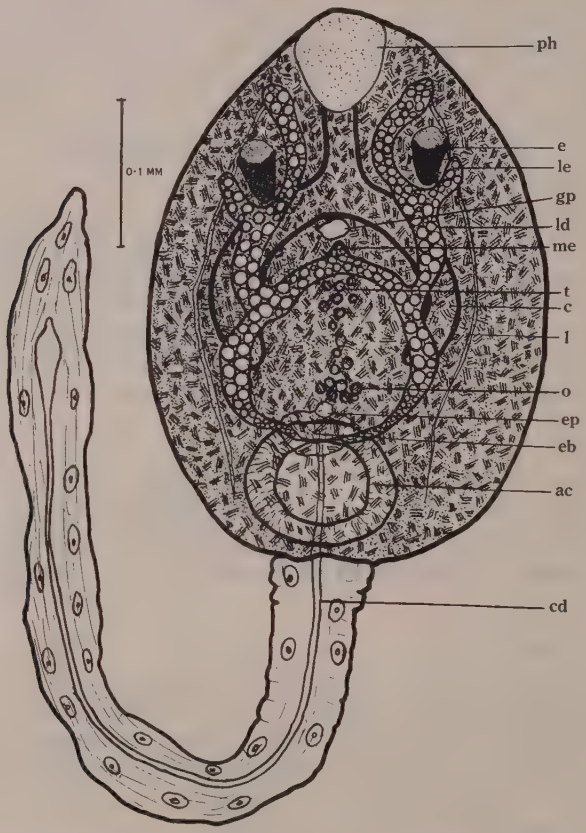


Fig. 9.—*Paramphistomum ichikawai.* Mature cercaria showing the internal structure (dorsal view); *ac,* acetabulum; *c,* caecum; *cd,* caudal excretory duct; *e,* eyespot; *eb,* excretory bladder; *ep,* excretory pore; *gp,* genital pore; *l,* lateral duct; *ld,* main lateral excretory duct; *le,* lateral evagination; *me,* median evagination; *o,* ovary; *ph,* pharynx; *t,* testes.

The cercaria of *P. ichikawai* differs distinctly from that of *C. streptocoelium* in the structure of the large lateral ducts of the excretory system. These are easily seen when the specimen is flattened between a slide and coverslip, and are defined by the presence of excretory granules similar to those seen in the cercariae of *C. streptocoelium.* The general arrangement of the ducts of the species is similar to that of *C. streptocoelium,* but a short median diverticulum is present running forwards from the centre of the cross anastomosis, and a

lateral diverticulum is given off from the main duct in the region of the eyespots, so that this part of the duct appears to surround the eyespot (Fig. 9). The main excretory duct continues forward and then backwards as a smaller duct containing a flagellum similar to that seen in *C. streptocoelium*. Flame cells were not seen in this species and were probably hidden by the opacity of the pigmentation and by the cystogenous cells.

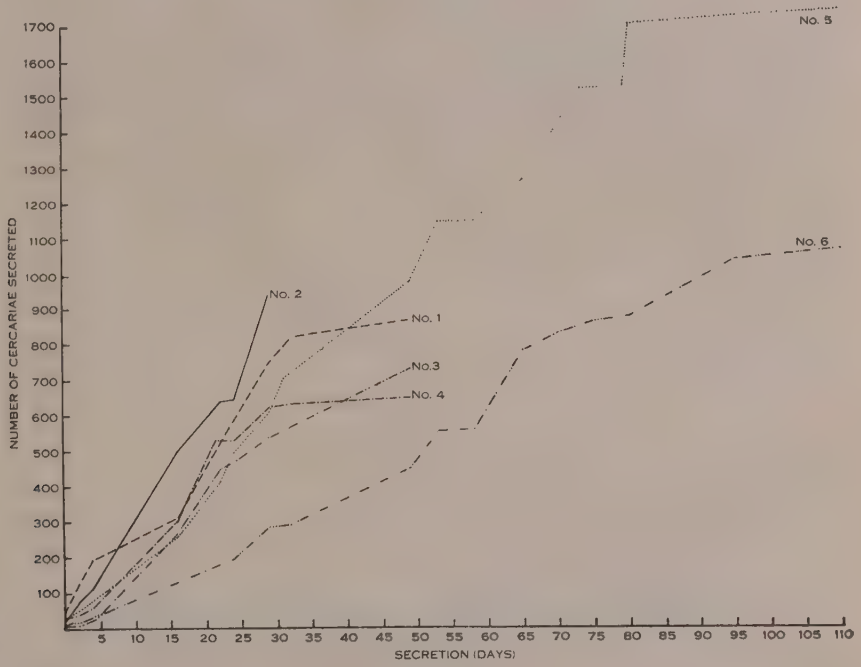


Fig. 10.—*Paramphistomum ichikawai*. Rates of secretion of cercariae of specimens of *S. alphena* infected in the laboratory with a single miracidium.

(2) *Rate of Secretion of Cercariae*.—To obtain an indication of the number of cercariae snails were capable of producing, specimens of *S. alphena* several days old were each infected with a single miracidium of *P. ichikawai* and were fed on the artificial snail food described by Standen (1951). The snails were isolated in 6 by 1 in. specimen tubes and maintained at a temperature of 20°C. Specimens were infected with miracidia on September 4, 1951 and secreted the first cercariae on October 14 and 15, 1951, i.e. 40 and 41 days after infection. The rate of secretion of cercariae is shown in Figure 10. All snails eventually died but were still secreting some cercariae at the time of death.

Figure 10 shows a somewhat constant rate of production of cercariae for the period of secretion, although the daily secretion rate varied considerably. It is probable that snails remain infected until they die, since in this trial snails reached diameters of 5-6 mm., corresponding favourably with the size of adult

snails from the field. Snails infected with mature cercariae taken from the field secrete cercariae at a rate somewhat similar to snails artificially infected in the laboratory. The rates of secretion are shown in Figure 11. These snails were also still secreting some cercariae at the time of death.

Snails 1 and 2 showed rates of secretion almost identical with those shown by the laboratory-infected specimens. The similarity between the results suggests that cercariae are secreted by snails at a somewhat similar rate irrespective of the degree of original infection and that the intensity reached by an infection with the larval stages depends not on the initial degree of infection but on the ability of the snail to carry the infection. This in turn is probably governed by the status of nutrition of the snail, the degree of infection in well-fed specimens being increased probably by the formation of daughter rediae.

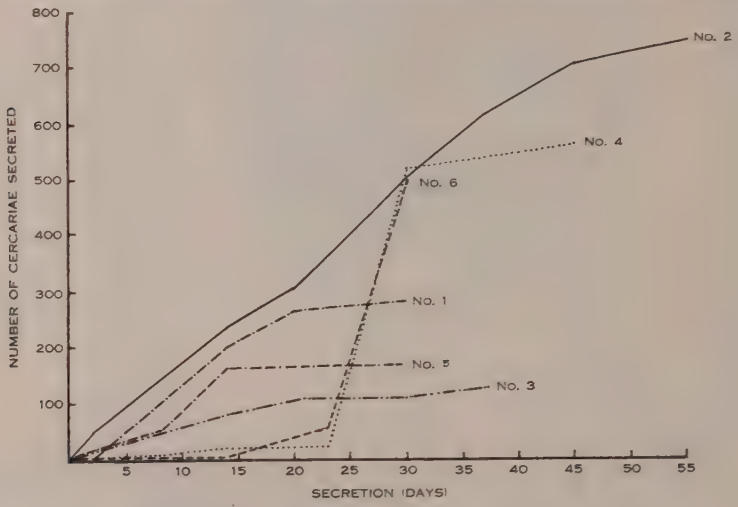


Fig. 11.—*Paramphistomum ichikawai.* Rates of secretion of cercariae of specimens of *S. alphena* collected from the field.

The rates of output of cercariae over short periods from snails agree to a large extent with the findings of Bennett (1936). This work considered the output of cercariae of *P. microbothrioides* as sporadic, in that, should a large number of cercariae be produced on one day, then very few would be produced during the next 1-8 days. The output of cercariae of *P. ichikawai* was obviously sporadic in that periods of high output followed by periods of low secretion were observed. However, this periodicity varied considerably from snail to snail, and in duration from 5 to 25 days.

(*c*) *The Metacercaria*

Cercariae behave in a similar manner to those of *C. streptocoelium,* being attracted by yellow light and not by green, red, or blue. Encystment normally takes place within 30 min. of liberation from the snail host and in a manner similar to that described for *C. streptocoelium.*

The metacercariae of *P. ichikawai* are brown to black and have a diameter of 226 μ across the base, with an embryo diameter of 166 μ, the embryo being slightly larger than that of *C. streptocoelium*. Cysts allowed to stand for 6 months under water showed a 32 per cent. viability.

(*d*) *Development in the Final Host*

Cysts of *P. ichikawai* were fed to sheep in which flukes became mature, as shown by faecal examinations, in 49 and 51 days.

A lamb was fed 1000 cysts of *P. ichikawai* on January 8, 1952, an additional 300 cysts on March 26, 1952, and a further 700 cysts on April 8, 1952. Eggs were first found in the faeces on February 28, 1952 and were undoubtedly laid by worms from the original 1000 cysts, which thus reached maturity in 49 days. The animal was slaughtered on May 1, 1952. On *post mortem* the rumen contained flukes of three size-groups, the largest group consisted of 361 specimens averaging 2.6 by 1.6 mm., an intermediate group of 77 specimens averaging 1.8 by 1.1 mm., and a small group comprising 18 specimens averaging 1.3 by 0.8 mm. Measurements were made on specimens fixed in 10 per cent. formalin. Twenty-seven specimens were collected from the small intestine and were scattered over the first 4 ft., the majority being recovered from the first foot. The mean measurements of these specimens corresponded closely with the smallest group in the rumen and were 1.3 by 0.8 mm.

These worms were in three well-defined size-groups and can be reasonably assumed to have originated from the three separate feedings of cysts. The smallest group at the date of slaughter was therefore 21 days old, and was distributed both in the intestine and the rumen. Specimens of this group still showed evidence of the pigmentation of the cercariae on the dorsal surface and it may be assumed therefore that migration from the intestine to the rumen commenced sometime within 3 weeks after infection. The second group was immature and was 34 days old, and as migration of this group had evidently been completed it may be presumed that all flukes would be in the rumen 34 days after infection.

The third and largest group was interesting in that only a few specimens of the 361 collected showed any eggs in the uterus. The testes were underdeveloped, and, in general, the whole genital structure presented a picture of immaturity. This group, however, must have been responsible for the eggs observed in the faeces previously, when counts as high as 175 eggs/g. of faeces were recorded. Possibly fluctuations in the egg output of this and other species of amphistomes are normal and are accompanied by changes in the genital system. Evidence of a similar rhythm in egg output has been observed in routine egg counts on a calf infected with a single infestation of cysts. The animal was infected for 180 days and during that time the egg count rose to a peak, fell to zero, and rose again to a similar peak about 65 days later.

That a rhythm in egg production may be normal in the life of the adult fluke is also shown by the frequent occurrence of specimens of all three species of amphistomes from natural infestations which had the dimensions and appearance of mature flukes but in which there was a marked lack of testicular de-

velopment associated with an absence of eggs in the uterus. The testicular degeneration in these specimens was most conspicuous, as in normal ovigerous specimens the testes occupy as much as half the space within the body. The specimens of *P. microbothrioides* recorded by Stunkard (1929) from antelopes as measuring up to 6 mm. in length and as being immature, may therefore have been collected during a period when egg production had ceased, in which case their apparent immaturity would not be associated with any host influence.

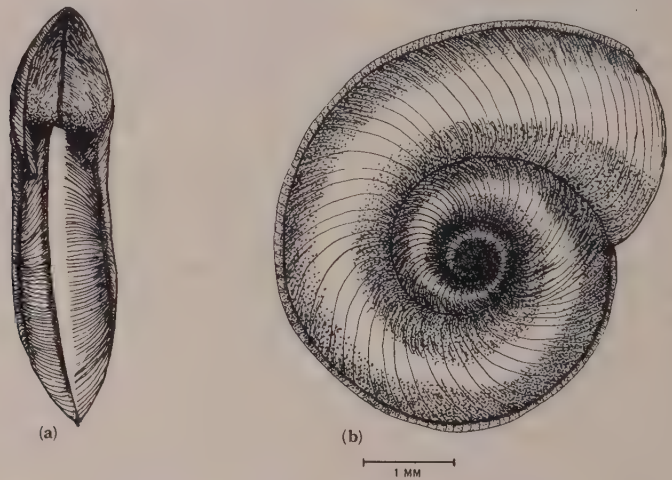


Fig. 12.—*Glyptanisus gilberti*. *a*, View showing mouth opening. *b*, View showing upper surface.

IV. Notes on the Bionomics of the Intermediate Hosts

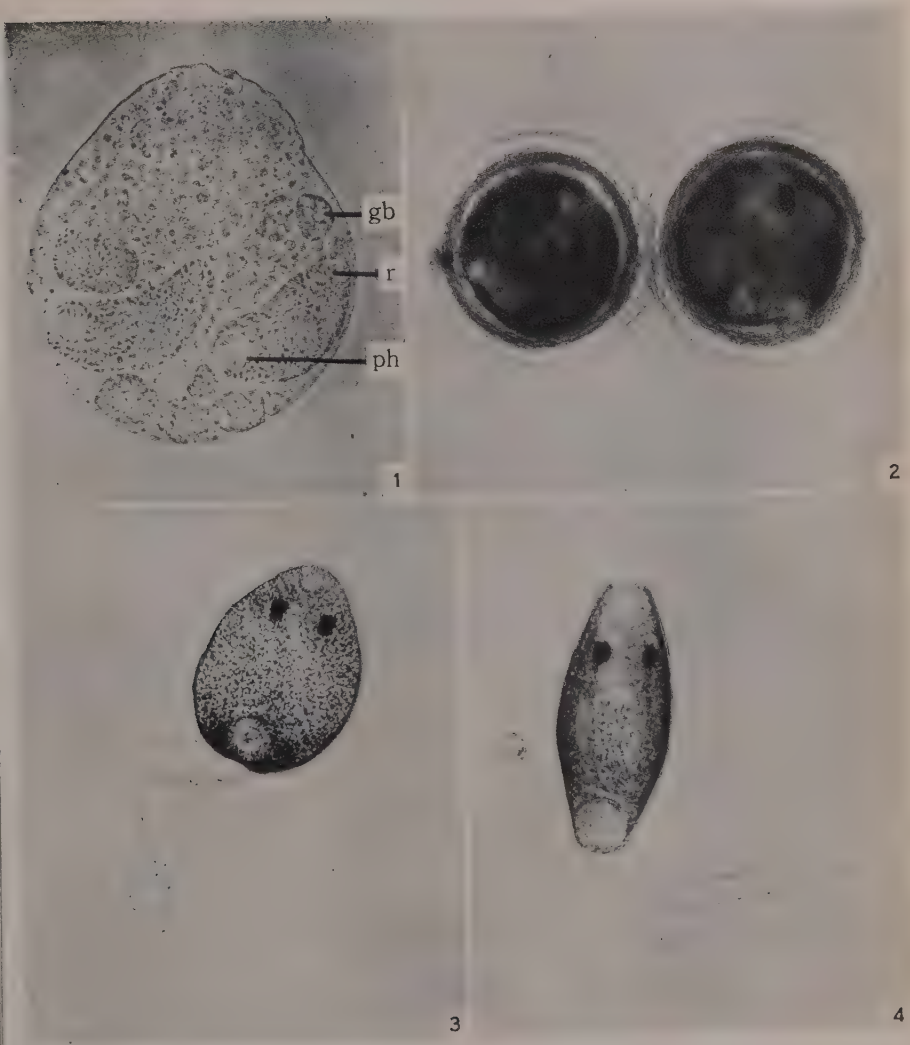
(*a*) *Differentiation of Species*

The snail intermediate hosts of *C. streptocoelium* and *P. ichikawai* are quite distinct in shell structure and can be readily recognized macroscopically.

Glyptanisus gilberti.—This freshwater snail (Fig. 12), which acts as the intermediate host of *C. streptocoelium*, has a small, brown, disc-like shell, somewhat resembling a ram's horn in shape (Fig. 12 (*b*)). It is typical of the family Planorbidae, and reaches 6-7 mm. in diameter, although specimens measuring 3-5 mm. are most commonly found in the field. Snails are flattened dorsoventrally with the central whorls slightly sunken and shells show marked lines of growth. The mouth is oblique (Fig. 12 (*a*)) and a keel is present around the periphery of the shell. The body of the snail is grey to reddish brown, with rounded foot, and the tentacles are thread-like.

Segnitilia alphena.—This freshwater snail, which acts as the intermediate host of *P. ichikawai*, is circular in shape and has a red to reddish brown shell. The lower surface of the shell is flat to slightly concave with a small central

PARAMPHISTOMES OF AUSTRALIAN RUMINANTS



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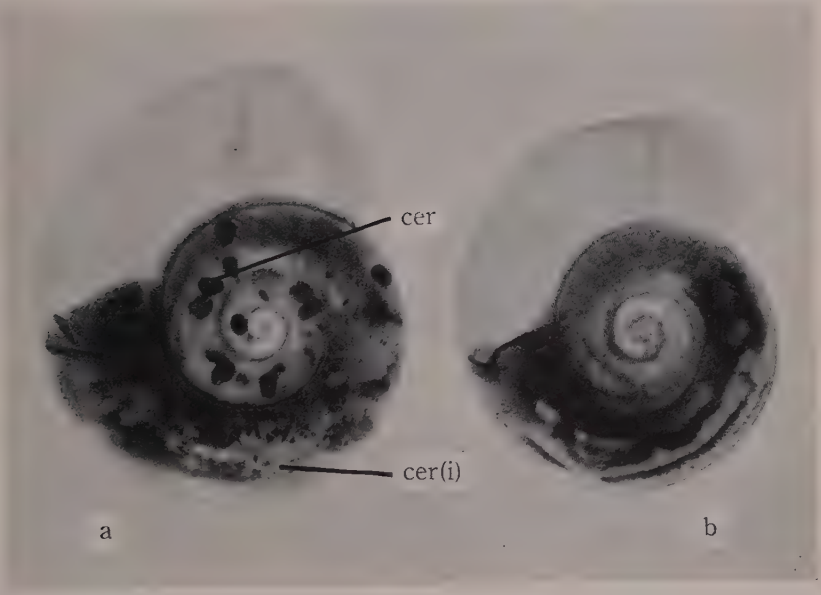

umbilicus (Fig. 13*b*). Snails measure up to 6 mm. in diameter but the majority from the field measure 3-5 mm. The shell presents a general glossy appearance and is unsculptured; growth lines are present but not conspicuous. The mouth is oval and teeth are absent (Fig. 13*a*). The body of the snail is red to reddish brown. This species has a rounded foot, and thread-like tentacles.

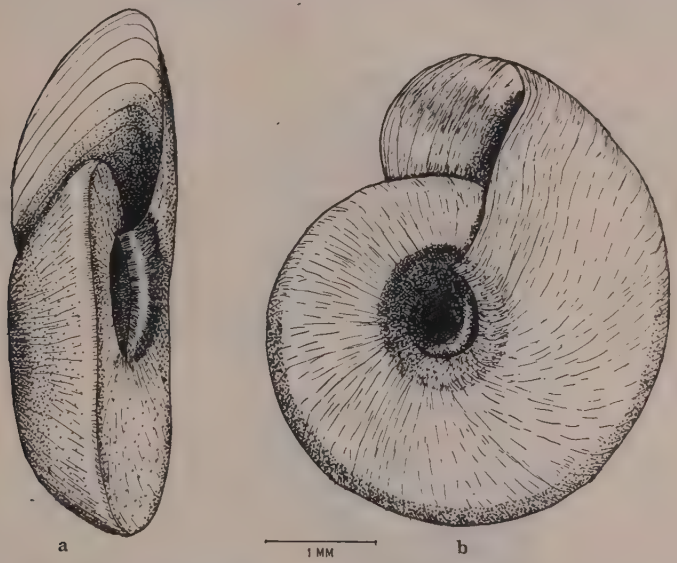

Fig. 13.—*Segnitilia alphena*. *a*, View showing mouth opening. *b*, View of lower surface showing central umbilicus

(*b*) *Bionomics*

These snails are small and inconspicuous so may easily escape detection and are most easily collected by means of a net. Both species may frequently occur together in the same habitats, which are quite variable in character. Large numbers are found in swamps and slow-moving streams, usually attached to grass or water weed in water 2-12 in. deep. They do not appear to be influenced by soil type or state of the water in the habitat to any great extent, as they are found in still water polluted by rotting vegetation as well as the clear water of flowing streams. Their distribution is widespread throughout the coastal and subcoastal regions of the eastern and southern States of Australia, where swamps and other areas of semi-permanent water abound.

These species feed mainly on microscopic algae, such as diatoms and desmids, but the chloroplasts of the various filamentous algae may also form a large proportion of the diet. In addition they may eat the tissue of the softer water plants, as they will attack boiled lettuce leaves readily in the laboratory.

Reproduction and egg-laying occur whenever conditions in the habitat become favourable for an increased population, and it has been found that

large snails taken in the field will deposit egg masses in the laboratory at any season when an adequate food supply is provided. The egg mass (Fig. 14) is attached to stones, sticks, plant stems, and leaves. It is oval in shape, convex on the upper surface, and flattened on the side of attachment. Egg masses deposited by large snails contain 10-16 eggs and measure 3-4 mm. in length but smaller ones may be produced by small snails which have recently reached maturity and may contain as few as two eggs.

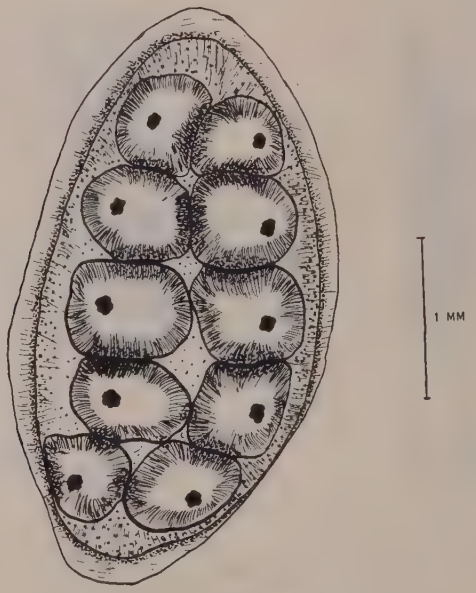

Fig. 14.—Planorbid egg mass (dorsal view).

The snails are pulmonates and breathe air in the adult stage, although in the very young stages the mantle cavity is usually completely filled with water, such specimens evidently utilizing dissolved oxygen. In young snails the pulmonary aperture is continually open and the water circulation within the mantle cavity is maintained by cilial action.

Both species are completely aquatic and rarely leave the water of the habitat to crawl on moist surfaces. It has been frequently noticed that snails in the laboratory left stranded on the sides of an aquarium by a retreating water level do not follow the receding water but die from desiccation in these positions. However, evidence from the field suggests that they do migrate with a falling water level to some extent, as there often appears to be an accumulation of dead snail shells around areas which are last to dry out. Repopulation of such areas when conditions become favourable is remarkably rapid. An instance of this was seen in a large swamp near Brisbane which, when visited in January 1952, was found to be completely dry with thousands of dead shells over the area. These conditions prevailed until March 1952, when rains made

the area habitable again. By July the snail population had once again become established in numbers almost equal to the original population and many snails collected at this time, especially specimens of *G. gilberti*, showed evidence by shell markings of having been present and alive during the drought period. Other snails collected were obviously of the post-drought period. How these snails survived is not known, but it is obvious that they have a remarkably efficient means of combating unfavourable habitat conditions.

V. Acknowledgments

The author wishes to express his appreciation of the cooperation received from the various officers of the State Departments of Agriculture of Queensland and New South Wales, who freely gave time and advice during the course of these investigations.

Thanks are also due to Miss J. Allan, Australian Museum, for her identifications of snail specimens on several occasions.

Thanks are also given for the helpful advice and criticism so willingly offered by Dr. F. H. S. Roberts, Officer-in-Charge of this Laboratory.

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—*Ceylonocotyle streptocoelium*. Mature sporocyst with well-developed rediae (× 150); *gb*, germ ball; *ph*, pharynx; *r*, redia.

Fig. 2.—*Ceylonocotyle streptocoelium*. Metacercaria (× 150).

Fig. 3.—*Paramphistomum ichikawai*. Mature cercaria flattened under a coverslip to show characteristic shape (× 70).

Fig. 4.—*Ceylonocotyle streptocoelium*. Mature cercaria flattened under a coverslip to show characteristic shape (× 100).

PLATE 2

Fig. 1.—*Ceylonocotyle streptocoelium*. *a*, Infected snail, *G. gilberti*. *b*, Uninfected snail of the same species (× 20 : *cer*, cercaria; *cer i*., immature cercaria.

THE DIFFERENTIATION OF THE INFECTIVE LARVAE OF SOME COMMON NEMATODE PARASITES OF CATTLE

By R. K. Keith*

[*Manuscript received December* 11, 1952]

Summary

Studies are reported on the differential diagnosis of the infective larvae of *Strongyloides papillosus, Haemonchus contortus, Ostertagia ostertagi, Trichostrongylus axei, Cooperia oncophora, C. punctata, C. pectinata, Bunostomum phlebotomum, Nematodirus* sp., and *Oesophagostomum* (*Bosicola*) *radiatum*, all of which occur in cattle in Queensland.

These larvae can be readily identified by the length and shape of the tail, assisted by body length, body width, certain head and tail structures, and by the presence or absence of a sheath.

A key for the identification of the larvae is given. Photographs of the larvae are also provided to assist identification.

I. Introduction

Studies by this Laboratory on parasitic gastro-enteritis of cattle are based mainly on faecal egg counts. Twenty-six species of nematodes have been recorded from the alimentary tract of Australian cattle and of these the eggs of only *Strongyloides papillosus* (Wedl 1856), *Ascaris vitulorum* Goeze 1782, *Bunostomum phlebotomum* (Railliet 1900), *Nematodirus* spp., and *Trichuris* spp. can be recognized with certainty in faecal examinations. Quantitative data on the remaining species are obtained from faecal cultures and differential counts on the infective larvae (Roberts and O'Sullivan 1951).

Many of the species recorded from cattle are of rare occurrence in Queensland. It has not been considered, therefore, of any practical value to attempt to study the infective larvae of such species as *Ostertagia occidentalis* Ransom 1907, *Trichostrongylus longispicularis* Gordon 1933, and *Cooperia spatulata* Baylis 1938, the infective larvae of which are unknown; nor to endeavour to ascertain whether the infective larvae of bovine strains of *O. circumcincta* (Stadelmann 1894), *T. colubriformis* (Giles 1892) Ransom 1911, and *C. curticei* (Railliet 1893) differ in any way from the published descriptions of those of ovine strains.

The nematodes commonly encountered include *Haemonchus contortus* (Rudolphi 1803), *O. ostertagi* (Stiles 1892), *T. axei* (Cobbold 1879) Railliet & Henry 1909, *S. papillosus, C. oncophora* (Railliet 1898), *C. punctata* (v. Linstow 1907), *C. pectinata* Ransom 1907, *B. phlebotomum, Oesophagostomum* (*Bosicola*) *radiatum* (Rudolphi 1803), and *Nematodirus* spp., and studies on the infective larvae have been confined to these.

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Several papers have been published on the morphology of the infective larvae of the common nematode parasites of sheep (Morgan 1930; Mönnig 1931; Dikmans and Andrews 1933), but little information is available on the infective larvae of the species commonly found in cattle. Conradi and Barnette (1908), Schwartz (1924), Krug and Mayhew (1946), and Sprent (1946) have described the infective larva of *B. phlebotomum,* Andrews and Maldonado (1941) that of *O. radiatum,* and Threlkeld (1946) that of *O. ostertagi.* The infective larvae of *C. punctata* and of *C. pectinata* were unknown, and those of *H. contortus, S. papillosus,* and *C. oncophora* were known only from sheep.

The measurements given by Dikmans and Andrews (1933) in the text do not always agree with those given in the tables. Where any discrepancy occurs the text measurements have been used by the author.

II. Methods

When studies of parasitic gastro-enteritis were first commenced some years ago, infective larvae of the common species of nematodes were studied from pure cultures of eggs (Roberts, unpublished data). The information given in this paper has been based on this earlier work but the measurements recorded were taken from larvae cultured from faecal samples from animals with mixed natural infestations. This method ensures that the range of measurements is more representative of each species than that given by measurements of larvae from a single pure culture.

The larvae were cultured according to the method used by Roberts and O'Sullivan (1951). They were conveniently prepared for examination by adding a small amount of iodine solution to the water in which they were suspended. Larvae killed in this way do not contract within the sheath, although many of them do not straighten out completely. It was found necessary to straighten larvae of *O. radiatum* by gentle heat, as iodine-killed specimens did not extend sufficiently well for measurement.

No attempt was made to make a detailed study of larval morphology and the author has been content to confine himself to characters useful for the quick diagnosis essential to routine larval differential counts. For this purpose the length and breadth of the larva, the length and shape of the tail of the sheath, the distance between the tip of the larval tail and the tip of the tail of the sheath, and the appearance of the anterior end proved most useful. Although after a little experience it is possible to differentiate most larvae under a magnification of about 36 diameters, occasionally a larva is seen which must be examined under a higher power for accurate differentiation. For this purpose a magnification of 100 diameters is most convenient.

The measurements recorded here were made on 100 larvae of each species except for *Nematodirus* spp., few larvae of which have been seen. As average measurements are of little significance, frequency distribution histograms have been constructed to show the range of measurements of the larvae.

Measurements for the length of the larva include the sheath, and measurements for the tail of the sheath were made from the anus to the tip of the sheath.

In the tables the term majority refers to 80 per cent. or more of the larvae. Photographs of the larvae and of the tails have also been provided as an aid to identification.

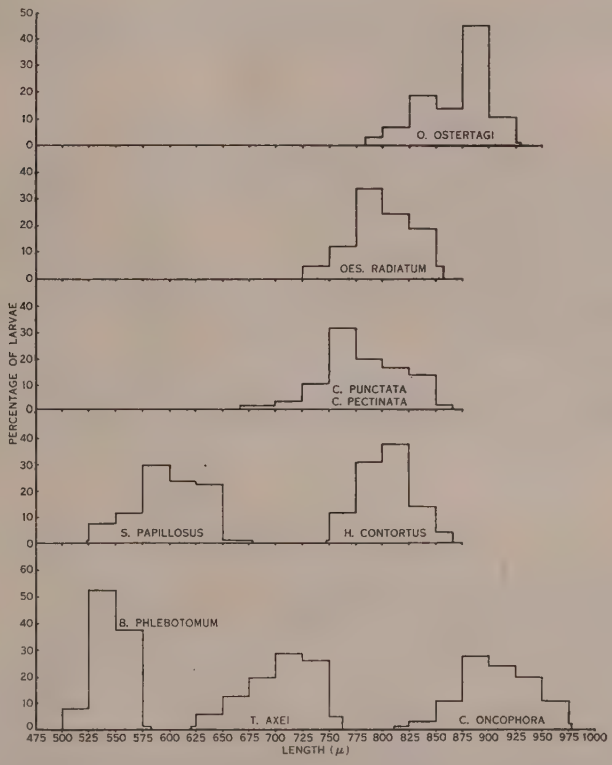


Fig. 1.—Infective larvae of nematode parasites of cattle. Frequency distribution of total lengths from the oral extremity to the tip of the tail of the sheath.

III. Descriptions of Infective Larvae

Strongyloides papillosus (Wedl)

Plate 1, Fig. 1

A description of the infective larva of this species from sheep has been given by several workers (Morgan 1930; Schwartz and Alicata 1930; Mönnig 1931). The infective larva from cattle conforms very closely in measurements and general morphology to that from sheep. The larva is slender, there is no sheath, and the oesophagus is very long, extending for 36-44 per cent. of the body length. Examination under high magnification shows that the tail is bifid.

Measurements made by the author are compared with those of other workers in Table 1. The frequency distribution of the author's measurements is shown in Figure 1.

TABLE 1

MEASUREMENTS OF THE INFECTIVE LARVA OF *STRONGYLOIDES PAPILLOSUS*

Host	Length of Larva (μ)		Max. Width (μ)	Authority
	Total Range	Range of Majority		
Sheep ..	574-710	—	15-17	Schwartz and Alicata (1930)
Sheep ..	598-675	—	—	Mönnig (1931)
Cattle ..	524-678	550-650	15	Keith

TABLE 2

MEASUREMENTS OF INFECTIVE LARVAE OF *BUNOSTOMUM* SPP.

Host	Total Length (μ)		Tail of Sheath (μ)		Extension of Sheath Beyond Tail of Larva (μ)		Authority
	Total Range	Range of Majority	Total Range	Range of Majority	Total Range	Range of Majority	
Sheep*	—	—	158	—	90-100	—	Morgan (1930)
Sheep*	560-637	—	133-153	—	—	—	Mönnig (1931)
Sheep*	514-678	—	153-183	—	85-115	—	Dikmans and Andrews (1933)
Sheep*	563-632	—	150-158	—	—	—	Ortlepp (1939)
Cattle†	580	—	—	—	—	—	Conradi and Barnette (1908)
Cattle†	500-540	—	—	—	—	—	Schwartz (1924)
Cattle†	450-580	—	—	—	60-90	—	Sprent (1946)
Cattle†	443-633	—	—	—	—	—	Krug and Mayhew (1946)
Cattle†	500-583	525-575	129-158	140-150	59-83	60-80	Keith

**B. trigonocephalum.* †*B. phlebotomum.*

Bunostomum phlebotomum (Railliet)

Plate 1, Fig. 2; Plate 3, Fig. 1

This is the smallest of the sheathed larvae to be seen in faecal cultures. The tail of the sheath tapers rapidly and runs out in a fine whip-like filament similar to that of the larva of *H. contortus*.

Measurements taken by the author are compared in Table 2 with those recorded by other workers for the larvae of this species and of *B. trigonocephalum.* The frequency distributions of the measurements of individual larvae of *B. phlebotomum* are shown in Figures 1, 2, and 3.

It seems from these measurements that the larva of *B. trigonocephalum* is slightly greater in body and tail measurements than the larva of *B. phlebotomum.*

Trichostrongylus axei (Cobbold) Railliet & Henry

Plate 1, Fig. 3; Plate 3, Fig. 2

The infective larva is medium in size and the tail of the sheath is short, conical, and bluntly pointed. Mönnig (1931) found he could not distinguish between the larvae of *T. axei, T. colubriformis* (*T. instabilis*), and *T. rugatus,* all of which came from sheep. Measurements given by Mönnig for these species, and those recorded by other workers for *T. colubriformis* and *T. vitrinus* from sheep are compared in Table 3 with the author's measurements for *T. axei* from cattle. Frequency distributions of the author's measurements for *T. axei* are shown in Figures 1, 2, and 3.

It is evident that the infective larva of *T. axei* from cattle conforms very closely to the descriptions and measurements given for this and other species from sheep.

TABLE 3

MEASUREMENTS OF THE INFECTIVE LARVAE OF *TRICHOSTRONGYLUS* SPP.

Host	Total Length (μ)		Tail of Sheath (μ)		Extension of Sheath Beyond Tail of Larva (μ)		Authority
	Total Range	Range of Majority	Total Range	Range of Majority	Total Range	Range of Majority	
Sheep*	656-772	—	86-110	—	—	—	Mönnig (1931)
Sheep†	674-749	—	86-105	—	25-38	—	Dikmans and Andrews (1933)
Sheep†	560-784	—	—	—	—	—	Gordon (1933)
Sheep‡	622-796	—	76-118	—	21-40	—	Dikmans and Andrews (1933)
Cattle§	619-762	650-750	83-107	90-100	25-39	25-39	Keith

* *T. axei, T. colubriformis, T. rugatus.* † *T. colubriformis.*
‡ *T. vitrinus.* § *T. axei.*

Haemonchus contortus (Rudolphi)

Plate 1, Fig. 5; Plate 3, Fig. 4

The infective larva from cattle is of medium length with a gradually tapering head. The tail of the sheath tapers to end in a whip-like filament of medium

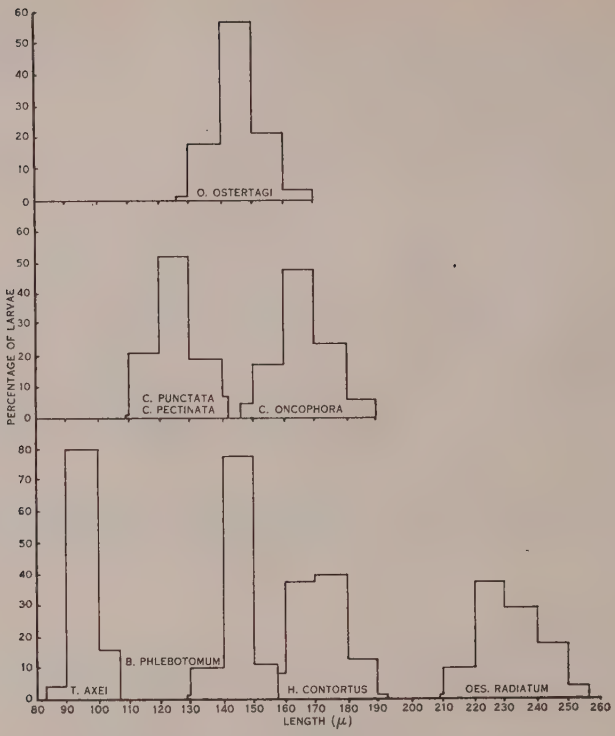


Fig. 2.—Infective larvae of nematode parasites of cattle. Frequency distribution of the lengths of the tail of the sheath.

TABLE 4

MEASUREMENTS OF THE INFECTIVE LARVA OF *HAEMONCHUS CONTORTUS*

Host	Total Length (μ)		Tail of Sheath (μ)		Extension of Sheath Beyond Tail of Larva (μ)		Authority
	Total Range	Range of Majority	Total Range	Range of Majority	Total Range	Range of Majority	
Sheep	—	—	—	—	70-84	—	Morgan (1930)
Sheep	694-772	—	145-165	—	—	—	Mönnig (1931)
Sheep	650-751	—	119-146	—	65-78	—	Dikmans and Andrews (1933)
Cattle	749-866	750-850	158-193	160-190	87-119	90-110	Keith

length. As in the infective larva from sheep there is usually a kink in the tail of the sheath immediately posterior to the tip of the tail of the larva.

Measurements made by the author are compared with those of other workers in Table 4 and their frequency distributions are given in Figures 1, 2, and 3.

The infective larva from cattle is longer and more robust than that from sheep and has a tail with a much longer whip-like filament (Plate 1, Fig. 4; Plate 3, Fig. 3).

Ostertagia ostertagi (Stiles)

Plate 2, Fig. 1; Plate 3, Fig. 5

The infective larva is one of the largest to be seen in faecal cultures though larvae of medium length frequently occur. The tail of the sheath tapers slowly to end in a blunt tip and is usually kinked immediately posterior to the end of the tail of the larva proper, giving the tail of the sheath a finger-like appearance. Under low magnification the part of the sheath extending beyond the tail of this larva often has a refractile appearance.

Measurements recorded by the author are given in Table 5, where they are compared with measurements given by other workers for this and other species of *Ostertagia*. Frequency distributions of the author's measurements for *O. ostertagi* are shown in Figures 1, 2, and 3.

TABLE 5

MEASUREMENTS OF INFECTIVE LARVAE OF *OSTERTAGIA* SPP.

Host	Total Length (μ)		Tail of Sheath (μ)		Extension of Sheath Beyond Tail of Larva (μ)		Authority
	Total Range	Range of Majority	Total Range	Range of Majority	Total Range	Range of Majority	
Sheep†	830	—	110	—	40-45	—	Morgan (1928, 1930)
Sheep*	888-907	—	110-121	—	—	—	Mönnig (1931)
Sheep*	656-880	—	—	—	—	—	Gordon (1933)
Sheep†	797-866	—	94-110	—	30-40	—	Dikmans and Andrews (1933)
Cattle‡	850-900	—	—	—	—	—	Threlkeld (1946)
Cattle	784-928	825-925	126-170	130-160	55-75	55-70	Keith

* *O. circumcinta, O. trifurcata.* † *O. circumcincta.*

‡ *O. ostertagi.*

It seems from these measurements that larvae of the genus *Ostertagia* are in general fairly large, and that larvae of *O. ostertagi* from cattle include some of the largest larvae. The tail of the sheath of larvae of *O. ostertagi* from cattle is also much longer and blunter than the tail of the sheath of larvae of *O. circumcincta* and *O. trifurcata* from sheep.

Cooperia punctata (v. Linstow) and *C. pectinata* Ransom

Plate 2, Fig. 2; Plate 3, Fig. 6

A study of the larvae of *C. punctata* in a pure culture showed that the tail of the sheath usually tapered gradually to end in a fine point, but occasionally the point was extended into a very short filament (Roberts, unpublished data).

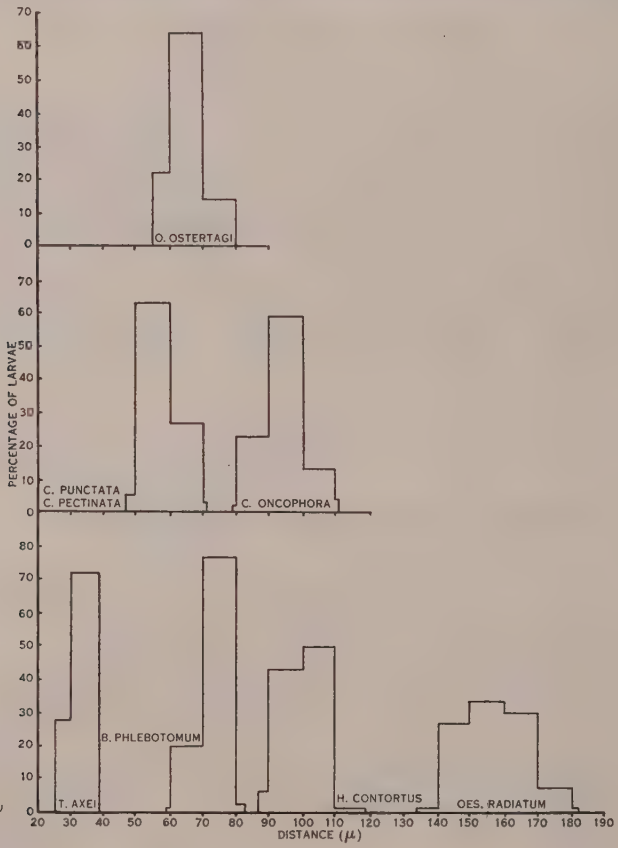


Fig. 3.—Infective larvae of nematode parasites of cattle. Frequency distribution of the lengths of the sheath extending beyond the tail of the larva proper.

In cultures from animals carrying *C. punctata* and *C. pectinata*, larvae are frequently seen with the tail of the sheath ending in a more conspicuous whip-like filament. The head characters of these larvae place them in the genus *Cooperia* and there is little doubt that they are the infective larvae of *C. pectinata*. It has, however, been impossible to separate the larvae of these two species on the appearance of the tail of the sheath as numbers of larvae with intermediate tail shapes and overlapping tail measurements are of frequent

occurrence. It has therefore been customary to combine the two species in differential counts and note the percentage of larvae of *Cooperia* spp. present.

Measurements by the author for *Cooperia* spp. give the larval length as 666-866 μ, the length of the tail of the sheath as 109-142 μ, and the extension of the sheath beyond the tip of the tail of the larva proper as 47-71 μ. The frequency distributions of these measurements are shown in Figures 1, 2, and 3.

Cooperia oncophora (Railliet)

Plate 2, Fig. 3; Plate 3, Fig. 7

This species also has a large infective larva, sometimes measuring about 1 mm. in length. The tail of the sheath is very characteristic, being long and tapering rather slowly and uniformly to end in a more or less blunt point. Some specimens have fairly fine tails to the sheath which appear intermediate between the usual tail for this species and the very fine whip-like tail of larvae of *H. contortus*.

The "two conspicuous oval bodies" at the anterior end of the oesophagus of the larvae of this species and of *C. curticei* referred to by Dikmans and Andrews (1933), and later described by Andrews (1935) as the optical cross section of a group of fibres surrounding the buccal capsule, have been seen in all three species of *Cooperia* studied by the author, namely *C. oncophora, C. punctata,* and *C. pectinata,* and are no doubt characteristic of the genus. Under low power this group of fibres appears as a transverse transparent band (Plate 3, Fig. 9).

TABLE 6

MEASUREMENTS OF INFECTIVE LARVAE OF *COOPERIA ONCOPHORA*

Host	Total Length (μ)		Tail of Sheath (μ)		Extension of Sheath Beyond Tail of Larva (μ)		Authority
	Total Range	Range of Majority	Total Range	Range of Majority	Total Range	Range of Majority	
Sheep	804-924	—	124-150	—	62-82	—	Dikmans and Andrews (1933)
Cattle	809-976	850-950	146-190	150-180	79-111	80-100	Keith

Measurements made by the author are compared in Table 6 with those recorded for this species by other workers. The frequency distributions of the author's measurements are shown in Figures 1, 2, and 3.

There does not seem to be any difference in the total length of the larvae examined by Dikmans and Andrews and those examined by the writer, but the larvae from cattle possess much longer tails. This may be indicative of a strain difference.

Oesophagostomum radiatum (Rudolphi)

Plate 2, Fig. 4; Plate 3, Fig. 8

This is a medium-sized larva in which the tail of the sheath tapers rapidly to end in a long, fine filament. The body has a rather stumpy appearance and specimens killed with iodine usually lie in a characteristic semicircular position. The sheath is coarsely ridged transversely and these ridges are very prominent on the inner edge of specimens lying in a curved position. Measurements taken by the author are presented in Table 7, where they are compared with those recorded for this species and for *Oesophagostomum columbianum* by other workers. The frequency distributions of the author's measurements for *O. radiatum* are shown in Figures 1, 2, and 3.

TABLE 7

MEASUREMENTS OF THE INFECTIVE LARVAE OF *OESOPHAGOSTOMUM RADIATUM* AND *O. COLUMBIANUM*

Host	Total Length (μ)		Tail of Sheath (μ)		Extension of Sheath Beyond Tail of Larva (μ)		Authority
	Total Range	Range of Majority	Total Range	Range of Majority	Total Range	Range of Majority	
Sheep*	791-849	—	204-235	—	—	—	Mönnig (1931)
Sheep*	771-923	—	193-235	—	125-160	—	Dikmans and Andrews (1933)
Cattle†	—	—	—	—	177	—	Andrews and Maldonado (1941)
Cattle†	726-857	750-850	209-257	220-250	134-182	140-170	Keith

* *O. columbianum.* † *O. radiatum.*

The larvae of these two species are apparently similar in total length, although the larvae of *O. radiatum* have tails which appear to be slightly longer than the tails of larvae of *O. columbianum.*

Nematodirus spp.

Plate 2, Fig. 5

Only a few larvae of *Nematodirus* have been seen as this is not a common parasite of cattle in the coastal and subcoastal areas of Queensland, from which the material for examination was drawn. They were probably larvae of *N. filicollis* as this species is seen to a greater extent than *N. spathiger* (Roberts 1939).

The larvae conform to the descriptions published by other workers and can be readily recognized by their large size and by the long, fine filament

in which the tail of the sheath ends. The dorsal and ventral wedge-shaped points with the slender prolongation between them at the tip of the tail of the larva proper, as described by Mönnig (1931), can be seen under high magnification.

The larvae measured 1095-1142 μ in length, the tail of the sheath 296-347 μ, and the extension of the sheath beyond the tail of the larva proper 207-266 μ.

IV. Discussion

With a little experience the larvae mentioned in this paper can be recognized under the low power of the microscope without much difficulty. In making the first differential counts of the day it is an advantage to examine several fields before attempting any count to get a comparative idea of tail length and appearance. Most larvae can be identified with ease by the appearance and length of the tail of the sheath alone.

Table 8

MEASUREMENTS OF INFECTIVE LARVAE OF SOME COMMON NEMATODES OF CATTLE

Species	Total Length (μ)		Tail of Sheath (μ)		Extension of Sheath Beyond Tail of Larva (μ)		Width (μ)
	Total Range	Range of Majority	Total Range	Range of Majority	Total Range	Range of Majority	
H. contortus	749-866	750-850	158-193	160-190	87-119	90-110	22-24
T. axei	619-762	650-750	83-107	90-100	25-39	25-39	22-24
O. ostertagi	784-928	825-925	126-170	130-160	55-75	55-70	24-28
C. oncophora	809-976	850-950	146-190	150-180	79-111	80-100	24-28
C. punctata / *C. pectinata*	666-866	725-825	109-142	110-140	47-71	50-70	22-24
B. phlebotomum	500-583	525-575	129-158	140-150	59-83	60-80	20
Nematodirus sp.	1095-1142	—	296-347	—	207-266	—	30
O. radiatum	726-857	750-850	209-257	220-250	134-182	140-170	28
S. papillosus	524-678	550-650	—	—	—	—	15

The length of the larva is not of any particular significance for most species but it helps in the identification of *Nematodirus* spp., *B. phlebotomum,* and the larger specimens of *O. ostertagi* and *C. oncophora.* The larvae of *Nematodirus* spp. and *O. radiatum* both possess very long filaments on the tail of the sheath. The former, however, may be recognized by their great length. Where any confusion exists in the differentiation of a larva of *T. axei* from a short-tailed one of *C. punctata,* or of a fine-tailed larva of *C. oncophora* or a long-tailed larva of *C. pectinata* from one of *H. contortus,* the head characters given for larvae of *Cooperia* spp. will readily distinguish between them. The absence of a sheath,

the slender body, and the long oesophagus, which shows as a transparent streak, give little difficulty in the identification of the larvae of *S. papillosus*. The larva of *B. phlebotomum* may be distinguished by its small size and the long *Haemonchus*-like tail of the sheath.

The width of the body usually has only a limited value in differentiation. The larvae of *Nematodirus* spp. and of *O. radiatum* have a width of about 30 and 28 μ respectively. The larvae of *O. ostertagi* and *C. oncophora* have a width of 24-28 μ, and those of *H. contortus, T. axei, C. punctata,* and *C. pectinata* a width of 22-24 μ. The larvae of *B. phlebotomum* are the most slender of the strongyle larvae with a width of about 20 μ, and the width of *S. papillosus* larvae is only 15 μ.

All the measurements recorded by the author are summarized in Table 8 and as a further aid to identification a key is given.

KEY TO THE INFECTIVE LARVAE OF SOME COMMON NEMATODES OF CATTLE

1. Sheath absent, oesophagus more than $\frac{1}{3}$ the length of the body *Strongyloides papillosus*
   Sheath present, oesophagus short 2

2 (1). Length including sheath less than 600 μ ..... *Bunostomum phlebotomum*
   Length including sheath more than 600 μ 3

3 (2). Tail of sheath less than 200 μ 4
   Tail of sheath more than 200 μ 5

4 (3). Two conspicuous oval bodies at anterior end of oesophagus 6
   No such structures at anterior end of oesophagus 7

5 (3). Length including sheath more than 1000 μ, tail of larva with dorsal and ventral lobes with a rod-like process between ..... *Nematodirus* sp.
   Length including sheath less than 1000 μ, tail of larva ending in a simple point ..... *Oesophagostomum radiatum*

6 (4). Length including sheath usually more than 850 μ, tail of sheath usually more than 150 μ long, tapering gradually to end bluntly ..... *Cooperia oncophora*
   Length including sheath usually less than 850 μ, tail of sheath tapering rapidly to a point or short fine filament less than 150 μ long ..... *Cooperia punctata*
   Cooperia pectinata

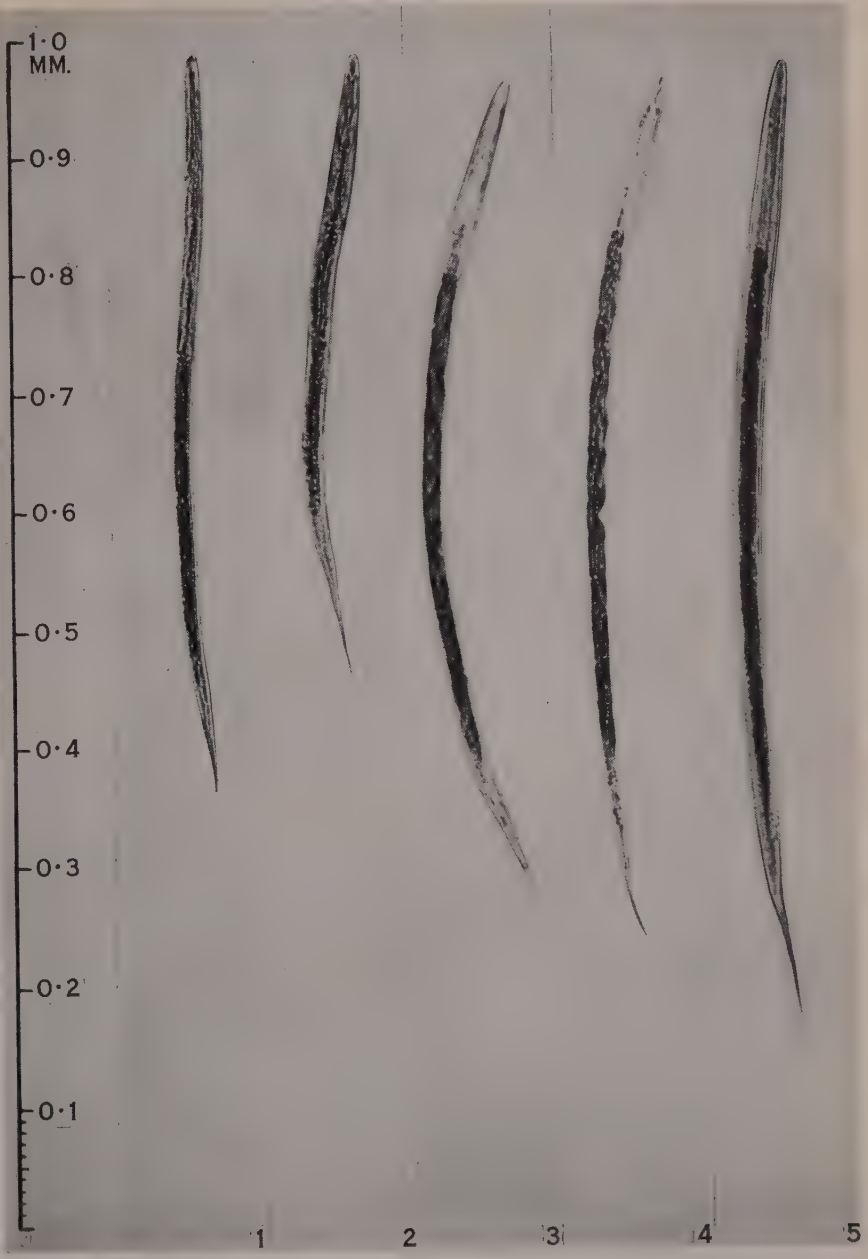
7 (4). Tail of sheath short and conical, less than 110 μ long ..... *Trichostrongylus axei*
   Tail of sheath longer, at least 126 μ long 8

8 (7). Tail of sheath ending bluntly ..... *Ostertagia ostertagi*
   Tail of sheath ending in a fine whip-like filament ..... *Haemonchus contortus*

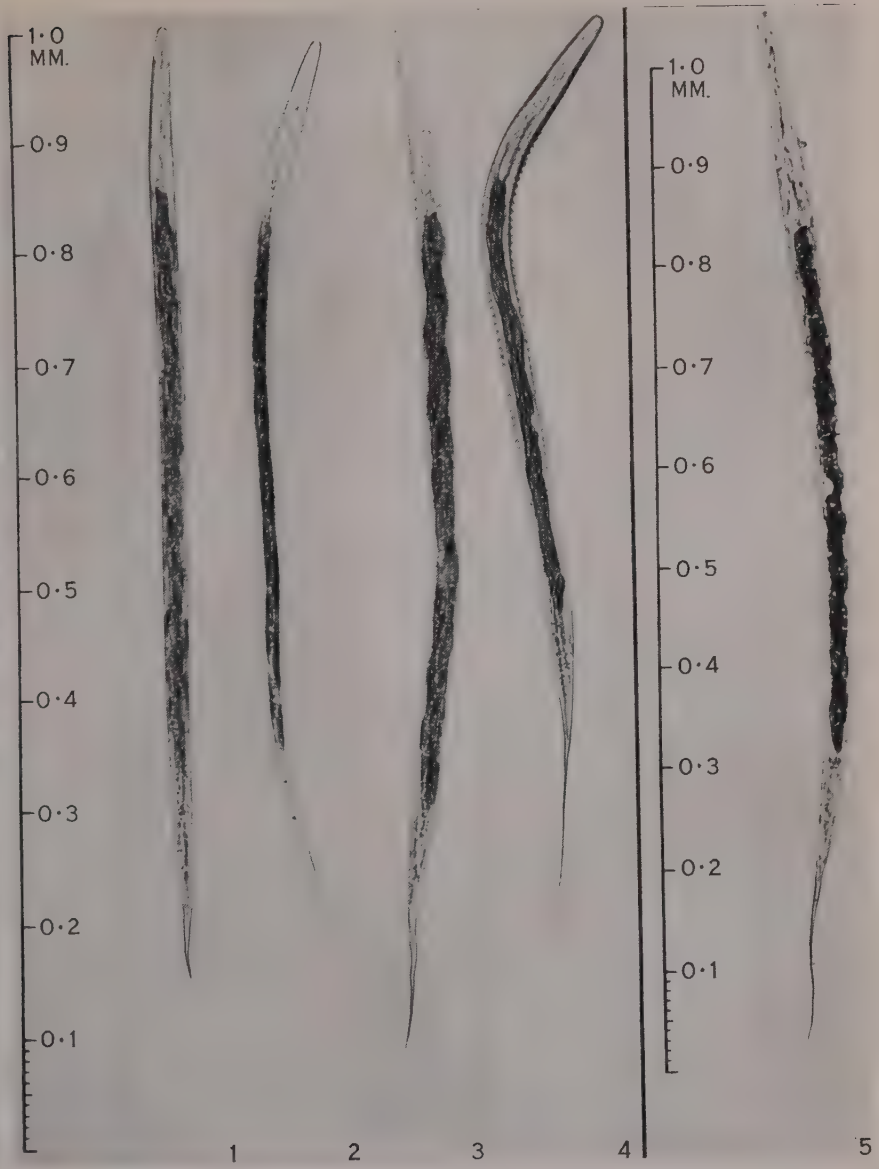
V. ACKNOWLEDGMENT

The writer wishes to express his thanks to Dr. F. H. S. Roberts for his advice and interest.

INFECTIVE LARVAE OF CATTLE NEMATODES



INFECTIVE LARVAE OF CATTLE NEMATODES



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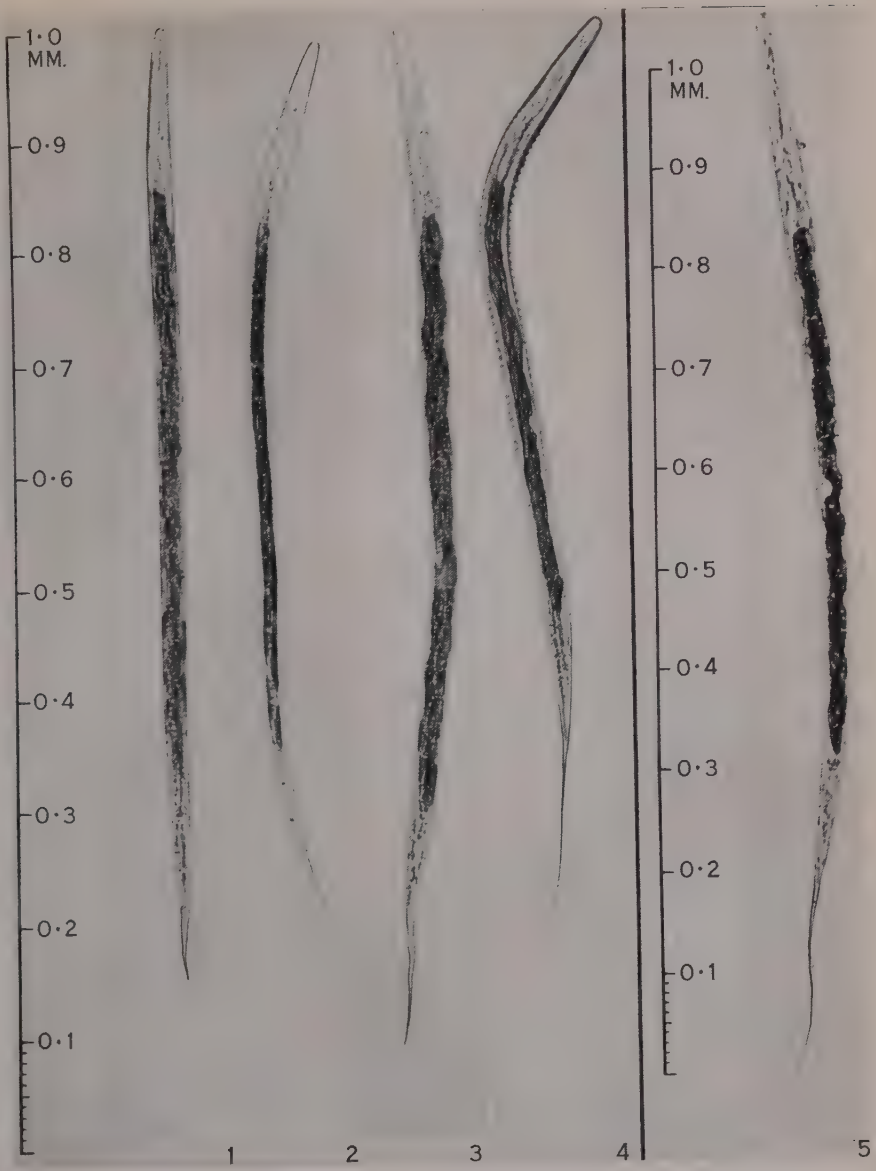
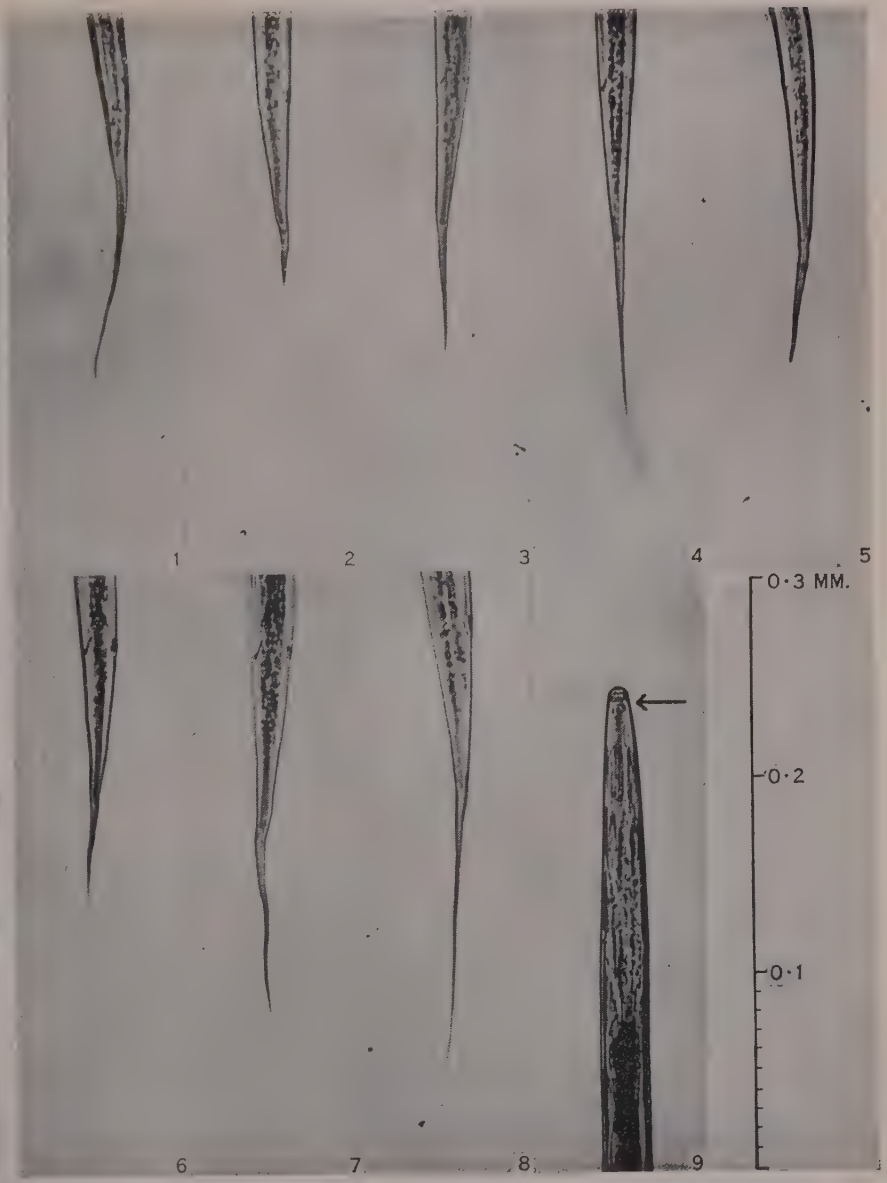


INFECTIVE LARVAE OF CATTLE NEMATODES



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Explanation of Plates 1-3

Plate 1

Infective larvae of nematode parasites of cattle.

Fig. 1.—*Strongyloides papillosus.*
Fig. 2.—*Bunostomum phlebotomum.*
Fig. 3.—*Trichostrongylus axei.*
Fig. 4.—*Haemonchus contortus* (sheep type).
Fig. 5.—*Haemonchus contortus* (cattle type).

Plate 2

Infective larvae of nematode parasites of cattle.

Fig. 1.—*Ostertagia ostertagi.*
Fig. 2.—*Cooperia punctata* and *C. pectinata.*
Fig. 3.—*Cooperia oncophora.*
Fig. 4.—*Oesophagostomum radiatum.*
Fig. 5.—*Nematodirus* sp. (separate scale).

Plate 3

Infective larvae of nematode parasites of cattle.

Fig. 1.—Tail of *Bunostomum phlebotomum.*
Fig. 2.—Tail of *Trichostrongylus axei.*
Fig. 3.—Tail of *Haemonchus contortus* (sheep type).
Fig. 4.—Tail of *Haemonchus contortus* (cattle type).
Fig. 5.—Tail of *Ostertagia ostertagi.*
Fig. 6.—Tail of *Cooperia punctata* and *C. pectinata.*
Fig. 7.—Tail of *Cooperia oncophora.*
Fig. 8.—Tail of *Oesophagostomum radiatum.*
Fig. 9.—Anterior end of *Cooperia* sp. The position of the group of fibres surrounding the buccal capsule is indicated by the arrow.

A NEW SPECIES OF ORIBATEID MITE FROM QUEENSLAND

By Marie Hammer*

[*Manuscript received October* 21, 1952]

Summary

A new species of oribateid mite, *Zygoribatula longiporosa*, is described from pastures in Queensland.

Introduction

A species of oribateid mite was received for identification from Dr. E. W. Baker, Bureau of Entomology, Department of Agriculture, Washington D.C., United States, to whom it had been sent by Dr. F. H. S. Roberts, Veterinary Parasitology Laboratory, C.S.I.R.O., Yeerongpilly, Queensland, Australia. Information supplied by Dr. Roberts indicated that this species was common in pastures in south-eastern Queensland.

Zygoribatula longiporosa, sp. nov.

Description.—Colour brown, length 0.53 mm., breadth 0.37 mm. Rostrum with a sharp tooth situated medianly on its anterior border and visible only on dissection (Fig. 1*C*). Rostral hairs rather thin and a little serrated, situated on small "hills" on a chitinized plate close to the lateral margins of the propodosoma in front of the tip of tectp. I and extending beyond the tip of the rostrum for about ⅔-¾ of their length. Lamellar hairs about ⅓ longer than rostral hairs, much thicker and rougher. Lamellae of equal thickness throughout their length. Translamella well developed, equal in thickness to the lamellae and forming a flat, posteriorly directed arch; inner margin of lamellae and translamella thickened; cuspes absent, but lamellar-translamellar junctions somewhat anteriorly directed. Interlamellar hairs stout, rough, erect, and anteriorly directed, a little longer than the lamellar hairs and slightly more slender. Pseudostigmatic organs directed laterally and anteriorly, club-shaped with fine setae, the stalk as long as the head and very slender. Tectp. I without a free tip, heavily striped.

Division between propodosoma and hysterosoma distinct.

Hysterosoma almost as broad as long, broadest near the middle and slightly pointed posteriorly, its anterior margin forming a flat, anteriorly directed arch which ends laterally in well-developed shoulders, each shoulder with a stiff, rough seta. Integument smooth; the dorsum with 11 pairs of short, stiff, rough setae disposed as in Figure 1*A*. Areae porosae distinct and unusual, the area porosa adalaris being very long and narrow, about ⅓ longer than the hairs, the area porosa mesonotica being as long as the hairs and the area porosa posteriora being of the common round shape (Fig. 1*A*). From the middle of the

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a.p. ad. and extending along the margin of the hysterosoma are many pale spots. The ventral aspect is shown in Figure 1*B*.

Tarsi with 3 claws, the median claw being the most powerful. Leg 4 is shown in Figure 1*D*.

Type specimens.—Two specimens (sex unstated) mounted together, labelled "Types, *Zygoribatula longiporosa* Hammer. In Pastures, Yeerongpilly, Queensland, Australia, May 14, 1952. From F. H. S. Roberts, Lot 52-5629." Deposited in the Queensland Museum.

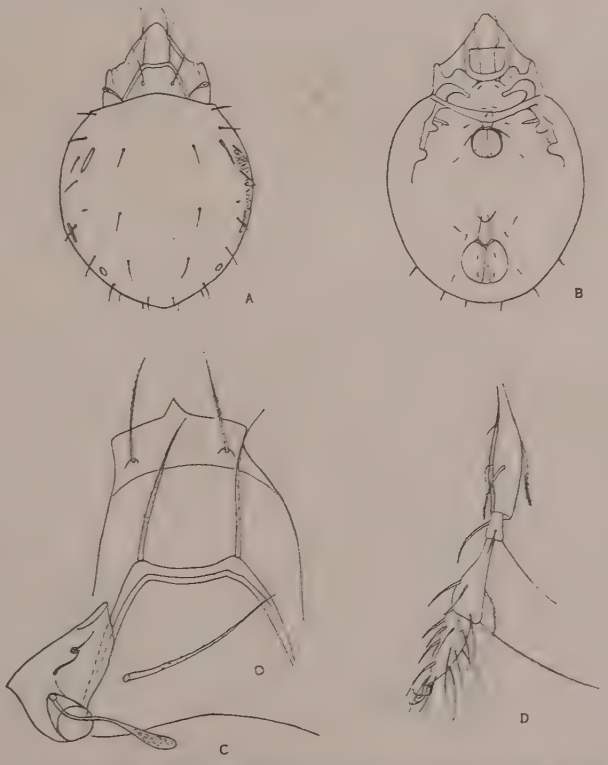

Fig. 1.—*Zygoribatula longiporosa*. *A*, dorsal view; legs are omitted. *B*, ventral view showing important morphological features; legs are omitted. *C*, dorsal view showing rostrum with its median tooth, rostral, lamellar, and interlamellar bristles, translamella, and pseudostigmatic organ. *D*, leg 4, from left side showing arrangement of setae and tarsal claws.

Discussion

Z. longiporosa is closely related to *Z. frisiae* (Oudemans), but differs from this species in several characters. The setae are rough in *Z. longiporosa* and very slender in *Z. frisiae*. The areae porosae adalaris and mesonotica are

elongate and narrow in Z. *longiporosa* and small and rounded in Z. *frisiae*, and the hysterosoma is rounded in Z. *longiporosa* and more oblong in Z. *frisiae*.

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ZYGORIBATULA LONGIPOROSA HAMMER (ORIBATEI:ACARINA), AN INTERMEDIATE HOST OF *MONIEZIA BENEDENI* (MONIEZ) (ANOPLOCEPHALIDAE : CESTODA) IN AUSTRALIA

By F. H. S. Roberts*

[*Manuscript received October* 21, 1952]

Summary

An examination of oribateid mites from cattle pastures in south-east Queensland showed *Zygoribatula longiporosa* Hammer to be the only species infested with cysticercoids. By feeding a number of these mites from a cattle pasture to a worm-free calf, the cysticercoids proved to be those of *Moniezia benedeni* (Moniez 1879).

Cysticercoids of a similar type were also found in *Z. longiporosa* collected from a sheep pasture.

I. Introduction

Moniezia benedeni (Moniez 1879) is the common cestode of cattle in coastal and subcoastal Queensland (Roberts 1939). Heavy infestations of this species frequently occur and field observations have indicated that, on occasions, these may be pathogenic. As a first step in investigations on the pathogenicity of this parasite it was necessary to determine an intermediate host so that pure infestations could be established in experimental animals.

Since the classical work of Stunkard (1937) involving mites of the supercohort Oribatei as intermediate hosts of anoplocephalide cestodes, 12 species have been recorded as vectors of species of *Moniezia*. Kates and Runkell (1948) list 10 species of Oribatei from records in the United States and Russia as intermediate hosts of *M. expansa*. These are distributed among the genera *Galumna, Oribatula, Scheloribates, Protoschelobates, Peloribates,* and *Adoristes*. *S. laevigatus* Koch, the only species listed by these authors in the genus *Scheloribates,* is also a vector in Canada (Rao and Choquette 1951). In Great Britain, *M. expansa* is carried by *Scutovertex minutus* Koch (Rayski 1947) and in India by *Scheloribates madrasensis* Koch (Anantaraman 1951). Four species are recorded as intermediate hosts of *M. benedeni,* namely *Galumna obvius* and *S. laevigatus* in Russia (Kates and Runkell 1948), and *S. madrasensis* and *Galumna* sp. in India (Anantaraman 1951).

II. The Oribateid Mite Fauna of Pastures

The observations recorded here were made in calf pastures in south-eastern Queensland during October 1951 to January 1952. A severe drought prevailed during this period but, despite these conditions, oribateid mites were recovered

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from the pastures in good numbers. The mites were isolated from turf samples by the modified Berlese funnel technique described by Kates and Runkell (1948).

Eight species of oribateid mites were recognized. *Zygoribatula longiporosa* Hammer and *Scheloribates* sp. were by far the most prevalent species. The former is a new species and a description of it is given by Dr. Marie Hammer elsewhere in this Journal. A large unidentified species of *Galumna* was present in the majority of the turf samples but was never numerous. The other five species of mites were comparatively rare.

III. The Intermediate Host of Moniezia benedeni

A summary of an examination of mites from the calf pastures is given in Table 1.

Table 1

EXAMINATION OF ORIBATEID MITES FROM CALF PASTURES FOR CYSTICERCOIDS

Locality	Species of Mite	No. Examined	No. with Cysticercoids	Percentage With Cysticercoids
Dayboro	*Zygoribatula longiporosa*	2430	45	1·8
	Scheloribates sp.	1369	0	0
	Galumna sp.	446	0	0
	Other species	210	0	0
Maleny	*Zygoribatula longiporosa*	1044	60	5·7
	Scheloribates sp.	1520	0	0
	Galumna sp.	339	0	0
	Other species	116	0	0

The majority of the infected Z. *longiporosa* had only a single cysticercoid each and the largest number of cysticercoids obtained from a single mite was seven. A cysticercoid from a mite from Dayboro is shown in Plate 1.

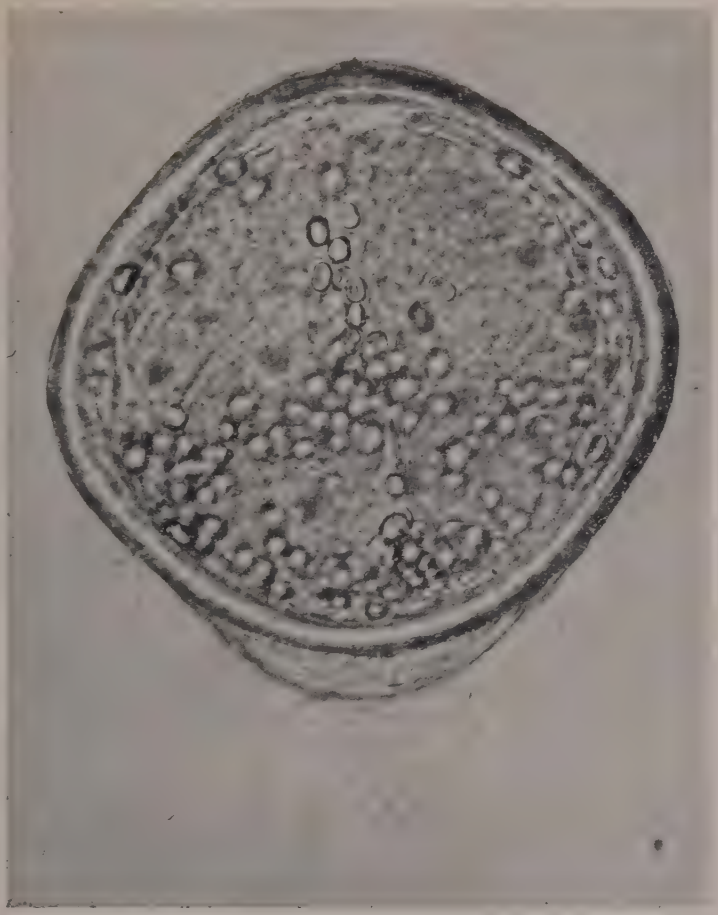
A number of Z. *longiporosa* from Dayboro was fed to a worm-free calf. Forty-two days later this calf passed a short chain of immature segments which were identified as *M. benedeni.*

IV. Discussion

The distribution of Z. *longiporosa* throughout the pastures was found to vary considerably. Some turf samples yielded large numbers of mites and others none at all. The mites appeared to be in greatest numbers in turf samples taken from dry areas and covered with short grass. As might be expected, the infestation rate among the collected Z. *longiporosa* also varied greatly. Some samples showed a high infestation rate, the highest being 21 per cent.; others did not yield a single infected mite.

The absence of cysticercoids in *Galumna* sp. was surprising in view of the role played by mites of this genus as intermediate hosts of *M. expansa* in the

ZYGORIBATULA LONGIPOROSA AS INTERMEDIATE HOST OF *MONIEZIA*



A cysticercoid of *Moniezia benedeni* (Moniez 1879) dissected from *Zygoribatula longiporosa* Hammer. × 450.

United States, where the only two known natural vectors of this cestode are *G. emarginatum* Banks and *G. virginiensis* Jacot (Kates and Runkell 1948).

It is of interest that cysticercoids have also been found in *Z. longiporosa* collected from sheep pastures at Yeerongpilly. *Scheloribates* sp. and *Galumna* sp. were again free from infection.

V. Acknowledgments

The writer wishes to acknowledge the assistance of Mr. W. Womersley, Entomologist, South Australian Museum, Mr. C. F. W. Muesebeck, U.S. Bureau of Entomology, and Dr. Marie Hammer, Hillerød, Denmark, for their assistance in the identification of the oribateid mites collected from the pastures.

The photograph of the cysticercoid was taken by Mr. R. K. Keith, Technical Officer, Division of Animal Health and Production, C.S.I.R.O.

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A REVIEW OF AUSTRALIAN NEMESTRINIDAE (DIPTERA)

By S. J. Paramonov*

[*Manuscript received July* 23, 1952]

Contents

Summary

The author has revised all material used by Mr. G. H. Hardy in 1924 and Dr. I. M. Mackerras in 1925 for their reviews of the Nemestrinidae as well as that accumulated during the last 25 years in the more important museum collections throughout Australia. One species of *Atriadops* from Aru I., as well as two species of *Exeretoneura*, one species of *Nycterimyia*, and 13 species of *Trichophthalma* from Australia, are described as new.

Additional descriptions and notes on the types of known species, as well as new locality records, have also been added.

A comprehensive key for the identification of both males and females of all species of *Trichophthalma* has been constructed. Previously, on the data available, it has only been possible to identify the male sex of many of the species with certainty.

The most important Australian genus, *Trichophthalma*, is represented by 45 species, while the Australian nemestrinid fauna now includes a total of 56 species.

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Introduction

Since the reviews of G. H. Hardy (1924) and of I. M. Mackerras (1925), Bequaert's paper entitled "The Nemestrinidae (Diptera) in the V.v. Roeder collection" (1932*a*) is the only important contribution to our knowledge of the Australian Nemestrinidae. The life history of *Trichopsidea oestracea* Westw. was studied by Miss M. Fuller (1938).

Bequaert's examination of the types in the von Roeder collection showed that the enigmatic species, *Rhynchocephalus ales* Newman 1841, is a representative of the genus *Hirmoneura* Meig., hitherto not recorded from the fauna of Australia. He also referred to another species of *Hirmoneura* from Queensland which, however, has not yet been described (see description of *H. ales* Newman below). This genus was thus omitted from both Hardy's and Mackerras's reviews.

Since the publication of Mackerras's paper much material has been accumulated in various Australian collections and this provides the basis for the present review.

In preparing this paper the author has had the opportunity of studying nemestrinids from the following collections: Division of Entomology, C.S.I.R.O., Canberra, including the nemestrinids collected in Western Australia by Mr. K. R. Norris, and the collection of Dr. I. M. Mackerras, which is preserved in the Division of Entomology Museum; the National Museum, Melbourne; the Australian Museum, Sydney; the New South Wales Department of Agriculture, Sydney; the School of Public Health and Tropical Medicine, Sydney; the Queensland Museum, Brisbane; the Queensland Department of Agriculture and Stock, Brisbane; the South Australian Museum, Adelaide; the Western Australian Museum, Perth; and the Western Australian Department of Agriculture, Perth. Many Australian types have thus been available for redescription or for the preparation of additional notes.

In this paper the author includes a new key for the determination of all the genera represented in Australia. He also describes one new species of *Atriadops* from Aru I. (which may occur also in New Guinea and in the northern part of Australia), two new species of *Exeretoneura,* one new species of *Nycterimyia,* and 13 new species of *Trichophthalma.*

This work was greatly facilitated by the earlier reviews, particularly that of Dr. I. M. Mackerras. Because of the very valuable general information on the family Nemestrinidae contained in Mackerras's paper, it has seemed unnecessary to include those details here.

Key to Australian Genera of the Family Nemestrinidae

1. Seven nearly parallel branches of veins reaching the anterior margin of the wing (1 subcostal, 4 radials, and 2 medians). Veins r_4 and r_5 bifurcated or (very rarely) conjoined in 1 point at the base. 2

   Four, 5, or 6 usually parallel branches of veins reaching the anterior margin of wing. Veins r_4 and r_5 mostly not bifurcated (bifurcated only in *Exeretoneura*) 3

2 (1). Proboscis at least at long as head. Eyes covered with dense and long hairs..... *Trichophthalma* Westwood

Proboscis much shorter than head, or nearly absent. Eyes (in Australian species either completely bare or with a few scattered microscopic hairs *Hirmoneura* Meig.*

3 (1). Veins r_4 and r_5 bifurcated. Six branches of veins reaching the anterior margin of wing. Eyes bare, markedly dichoptic in both sexes. Third antennal joint quite atypical; longer and broader than the basal joints, with 5 rings at tip, tabanid-like; r_{2+3} and r_4 are joined by 1 interradial cross-vein..... *Exeretoneura* Macquart

Veins r_4 and r_5 not bifurcated. Only 5 branches of veins reaching the anterior margin (in *Cyclopsidea* the 6th reaches the hind margin just beyond the tip of wing). Third joint of antennae is usually thin, swollen at base (and at apex in *Cyclopsidea*).....4

4 (3). Ocelli absent. Axillary cell extremely large, much broader than anal cell, with a broadly rounded exterior margin; vein 2A (2nd anal) present, running from base of cell to middle of hind margin. Wings dark, spotted. Metatarsus as long as the last tarsal joint.....*Atriadops* Wandolleck

Ocelli distinctly developed. Axillary cell very small, no broader than anal cell, or if it is broader, its hind margin is not regularly rounded. Only a short (basal) part of 2nd anal vein present 5

5 (4). Veins m_1 and m_2 conjoined at a distance from the anterior margin of wing. Anal cell nearly closed at apex. Wings hyaline.....*Trichopsidea* Westwood

Veins m_1 and m_2 running parallel to the anterior margin of wing. Anal cell very widely opened at apex. Wings coloured, hyaline in *Cyclopsidea* only.....6

6 (5). Axillary cell extremely long and narrow, narrower than the anal cell at apex, and with a concave hind margin 7

Axillary cell much broader than the anal cell, long, but with a distinctly convex hind margin. Hind femora swollen towards the apex.....*Nycterimyia* Lichtwardt

7 (6). Wings dark, with some hyaline spots. Hind margin of wing forming a very distinct angle. The veins running towards the apex of wing are slightly S-shaped, not straight. Apex of 3rd antennal joint acute. Five branches of veins (4 of which are readily visible) reaching the anterior margin of wing. Hind tibiae extremely swollen, thicker than the hind femora ..... *Nycterimorpha* Lichtwardt

Wings hyaline. The hind margin of wing is usually very evenly rounded. All veins which run towards the apex of wing are straight and parallel. Apex of 3rd antennal joint club-shaped. Five branches of veins reaching the anterior margin of wing, and the 6th a little beyond the tip of wing. Hind tibiae distinctly narrower than the hind femora ..... *Cyclopsidea* Mackerras

1. Genus NYCTERIMYIA Lichtwardt

Nycterimyia Lichtwardt, 1909, Dtsch. ent. Z., p. 647.

Seven species of this genus are now known: *N. dohrni* Wand. (generotype) from Andaman Is., *N. kerteszi* Lichtw., *N. fenestro-clathrata* Lichtw., and *N. fenestro-inornata* Lichtw. from Formosa, *N. papuana* Beq. from New Guinea and *N. horni* Lichtw. from Queensland; and a new species from Queensland is described below.

* *Ceyloniola* Lichtwardt-Strand from Ceylon differs by its cross-banded wings and extremely large axillary cell, which is at least 3 times as broad as anal cell.

Although Mackerras has not seen *N. papuana* Beq., he quoted its full description.

KEY TO SPECIES OF THE GENUS NYCTERIMYIA

1. Wings uniformly brownish or reddish brown, without hyaline spots. Alula dark. Hind margin of wing has 2 sharply marked angles at apex of "diagonal" vein (m_{3+4}) and at apex of anal cell. The veins m_{1+2} and r_{4+5} are curved downwards before the apex. Formosa.....*N. fenestro-inornata* Lichtw. ♂

Wings brownish, always with hyaline spots of different shape and size.....2

2 (1). Basal part of axillary cell always with a large hyaline spot near alula; there is also at least 1 hyaline spot in the 1st submarginal cell.....3

Whole axillary cell dark. Only 1 hyaline spot, narrow, somewhat curved in the 4th posterior cell (the cell immediately below the discal cell), moreover there are some subhyaline areas: in the 2nd basal cell and in the combined 1st and 2nd posterior cells. New Guinea.....*N. papuana* Beq.

3 (2). No hyaline spot in discal cell. Tip of wing with hyaline spots. Alula dark.....4

A large hyaline spot in basal part of discal cell. Tip of wing with hyaline spots. Alula white.....6

4 (3). Wing with 3 large triangular hyaline spots: 1 occupying the most part of the 2 basal cells, 1 at hind border of wing in area in front of anal cell, and the last occupying the most part of submarginal cells (at base). Queensland *N. commoni*, sp. nov. ♀

Wing with only 1 large triangular spot at base of submarginal cell.....5

5 (4). Hyaline spot in axillary cell apically very excavated. A very small hyaline spot may be present or absent in 2nd ½ of 2nd basal cell. Queensland *N. horni* Lichtw. ♂

Hyaline spot in axillary cell apically nearly straight. A very large hyaline spot in the 2nd basal cell. Sumatra, Andaman Is. .....*N. dohrni* Lichtw. ♂

6 (3). Veins m_{1+2} and r_{4+5} distinctly curved upwards at apex. A hyaline spot in the upper acute corner of cell between r_{2+3} and r_{4+5}. Formosa.....*N. kerteszi* Lichtw. ♀

Veins m_{1+2} and r_{4+5} straight or only slightly curved downwards at apex. Formosa ... *N. fenestro-clathrata* Lichtw. ♀

NYCTERIMYIA HORNI Lichtwardt

Fig. 1

Nycterimyia horni Lichtwardt, 1912, Ent. Mitt. 1: 27, fig. 1.

The author has seen specimens from Toowoomba, south Queensland (1 ♂, 10.ii.1927, W. B. Barnard) and Palm. I., north Queensland (3 ♂♂, 20.xii.1930-6.i.1931, I. M. Mackerras).

It is very probable that *N. horni* is only a subspecies of *N. dohrni* or even a synonym of this species. Sufficient material is not yet available to enable this question to be decided definitely.

Ground colour of body reddish brown, only the eyes dark brown; halteres and antennae yellow. Upper ⅔ of eyes with larger facets than in the lower ⅓. Eyes nearly contiguous. Ocellar triangle very prominent, with very large lateral ocelli. The long reddish brown hairs on the triangle are curved forwards. Antennae as in Figure 15*a* of Mackerras. The short frons (which is as long as

the connecting line of the eyes), the basal joints of antennae, and face are covered with long, dense, reddish brown hairs; similar hairs cover the thorax and abdomen; in some places they are a little darker, in others paler.

The hairs on mesonotum are directed backwards, on the scutellum upwards and a little forwards.

Hind femora in their distal ½ swollen, the hind tibiae at apex also a little thickened. Tarsi comparatively short. The length of the hind metatarsus is a little greater than the combined length of the next 3 tarsal segments.

Venation and pattern of wing as in Figure 1 of Lichtwardt (1912) but the small spots in the 2nd basal cell and in the 4th posterior (below the discal cell) nearly or quite absent. The hyaline spot in axillary cell is variable in shape, from distinctly excavate to nearly straight.

Abdomen above with 2 parallel rows of yellow spots on 2nd to 6th tergite, which are only a little paler than the remaining surface, but they are shining and when viewed from the side can have a white or whitish reflection. The hind borders of sternites and tergites (especially the latter) are swollen. Genitalia asymmetrical, very large, swollen.

Length of body 11 mm., of wing 12 mm.

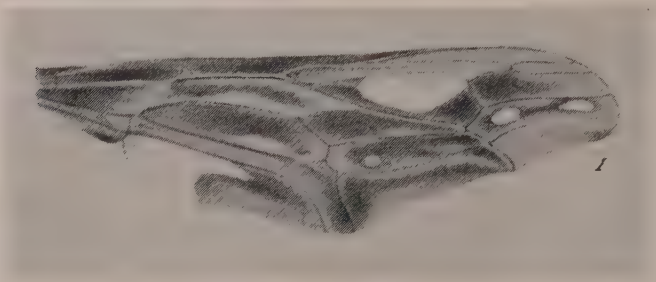

Fig. 1.—*Nycterimyia horni* Lichtw. (after Lichtwardt).

NYCTERIMYIA COMMONI, sp. nov. ♀

Fig. 2

A representative of a new group of species, having 3 very large triangular hyaline spots on wing.

Ground colour of body dark brown with dense, but not long, goldish hairs on head, thorax, and the upper side of abdomen; legs, halteres, antennae, and the under side of abdomen yellow.

Vertex nearly as broad as ocellar triangle. Frons rather broad, at base of antennae nearly equal to ¼ of head width, the lower ½ of frons with long and dense golden hairs, face with similar hairs.

Wings dark brown, with 5 hyaline spots (3 large, triangular, and 2 much smaller).

The 1st large spot occupies the greater part of the lower basal cell (only the base and apex are a little darkened) and a little more than the median ⅓ of the upper basal cell; the 2nd, situated in front of anal cell, is triangular in shape with its apex penetrating the cell beneath the discal cell; the 3rd triangular spot occupies the greater part (with the exception of the apex) of the cell between $r_{2\text{-}3}$ and $r_{4\text{-}5}$ (its basal part, which is clearly separated from the apical by a supernumerary cross-vein); a part of this spot penetrates into basal part of the cell between r_1 and $r_{2\text{-}3}$, which is also well separated from the apical part by a supernumerary vein. A small hyaline spot is also situated at apex of the cell between the vein $r_{4\text{-}5}$ and $m_{1\text{-}2}$. Another hyaline spot is at base of the axillary cell, occupying nearly ¼ of its length.

Alula very narrow, black. Two cells at tip of wing between $r_{4\text{-}5}$, $m_{1\text{-}2}$ and the hind margin are broader and shorter than in Figure 15 of Mackerras, but the venation in general is very similar.

Ovipositor a little shorter than the anterior femora. Legs comparatively much shorter than in *N. horni*, and the femora more swollen. Tarsi comparatively shorter and thicker.

Length of body 9 mm., of wing 11 mm.

1 ♀, 28.ii.1950, Yeppoon, Queensland (I.F.B. Common).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

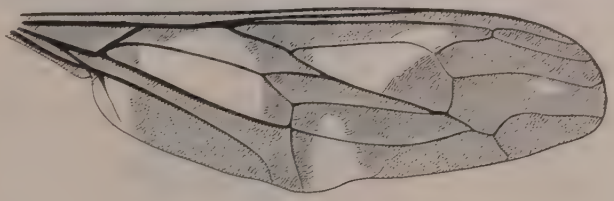

Fig. 2.—*Nycterimyia commoni*, sp. nov.

2. Genus NYCTERIMORPHA Lichtwardt

Nycterimorpha Lichtwardt, 1909, Dtsch. ent. Z., p. 648.

This is a very inadequately studied Australian and Malayan genus. Genero-type: *N. speiseri* Lichtw. from Cairns, Queensland, in the collection of Lichtwardt; a 2nd specimen of this species from Tambourine Mt., Queensland, in the Queensland Museum. A 2nd species (*N. pyralina*) was described by Edwards (1932) from Singapore. Dr. I. M. Mackerras quoted Lichtwardt's description in full. Edwards's figures of the wings of *N. speiseri* and *N. pyralina* are reproduced in Figures 3 and 4.

Nycterimorpha speiseri Lichtwardt ♂

Fig. 3*b*

Nycterimorpha speiseri Lichtwardt, 1909, Dtsch. ent. Z., p. 648.

The author has seen 5 males from the following localities: 1 ♂, 31.x.1927, Green I., Queensland (F. Roberts); 1 ♂, 29.xi.1925, Tambourine Mt., Queens-

land (H. Hacker); 1 ♂, Mar., Tambourine Mt., Queensland (E. J. Dumigan); 1 ♂, Tambourine Mt., Queensland (W. H. Davidson); 1 ♂, 25.i.1926, Tooloom, N.S.W. (H. Hacker).

The ground colour of the body is yellow, rather bright or in some specimens a little darker, brownish. The abdomen is very soft and can be easily deformed. Head short and transverse. Ocellar triangle small, nearly equilateral. The facets in the upper ½ of eye are very large, and gradually decrease in size towards the lower margin where they are much smaller. Eyes dark brown. The connecting line of the eyes is short, nearly twice as long as the ocellar triangle, but incomplete: there is a microscopic narrow dividing stripe. Frons triangular, much higher than it is wide, with erect, very soft, yellow hairs. The upper side of the 3rd antennal joint is distinctly haired (from the base to the apex); the hairs are very fine, yellowish. The 2nd joint is quadrate, a little longer than the 1st, which is very short; the 3rd is very thin, flagelliform, ½ as broad as the 2nd.

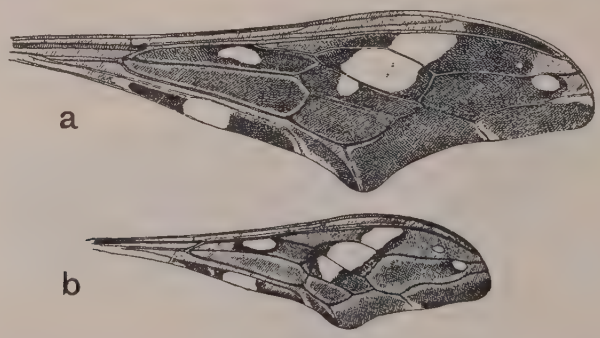

Fig. 3.—*a, Nycterimorpha pyralina* Edw.; *b, N. speiseri* Lichtw. (after Edwards).

The face of a very characteristic form: it is the shape of a distinct conical tubercle, separated from the sides (genae) and the flat upper part; in profile the face is egg-shaped. Apical joint of palpi protruding, but not reaching the apex of the face. Proboscis absent. Head is 1.5 times as broad as high. Occiput with sparse yellowish pubescence.

Thorax yellow, but the mesonotum a little darker, and there are also paler and darker irregularly placed markings on the sides of thorax. Hairs on mesonotum and scutellum extremely fine, yellowish. Scutellum extremely large. Legs yellow, tarsi semi-pellucid. The anterior and middle pairs of legs normal, but the hind tibiae very swollen, thicker than the hind femora. Halteres yellowish, extremely long. Wings with very peculiar venation and pattern (Fig. 3).

Mackerras did not examine a representative of this genus, and his Figure 16, modified from Hardy and Lichtwardt, is therefore incorrect.

The apical part of the anal cell is situated before the sharply marked angle of the hind margin of the wing, and not after it. The figure of *N. speiseri* of Edwards is very exact, but in each of the 5 specimens examined by the author, the vein which closes the discal cell distally is distinctly nearer the base of *r* than in Figure 6 of Edwards; its position is similar to that in Figure *a*.

The hind margin of wing from the apex of anal cell is occupied by a row of very small black tubercles (as black points).

Abdomen long, narrow, with 7 distinctly visible laterally compressed segments, yellow or brownish; on the anterior border of the 2nd to the 5th tergites there are pairs of gradually diminishing nearly white spots. Genitalia very peculiar: they are nearly covered by the last sternite, which curves up towards the upper side.

Length of body 8-9.5 mm., of wing 9-11 mm.

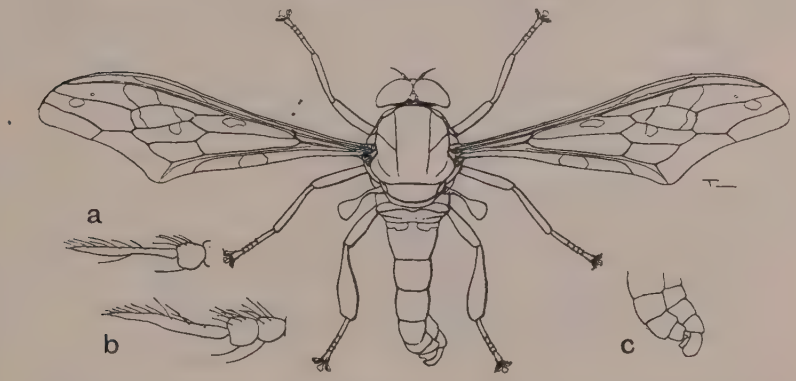

Fig. 4.—*Nycterimorpha pyralina* Edw. *a*, Antenna of *N. speiseri* Lichtw.; *b*, antenna of *N. pyralina* Edw.; *c*, tip of abdomen of *N. pyralina* Edw., side view (after Edwards).

3. Genus EXERETONEURA Macquart

Exeretoneura Macquart, 1846, Dipt. Exot. Suppl. 1: 105.

The position of this genus in the family Nemestrinidae is, in the author's opinion, not definite. Many characters separate the genus from other genera of Nemestrinidae: the long, annulated 3rd antennal joint, the flat mouth cavity which is placed in a deep depression in the head, bare eyes, 2 spurs at apex of middle and hind tibia, the vein r_1 which is haired from the base to the apex, the unusual form of the cell below the discal cell, the absence on the 1st 4 tergites of small hairless spots, and the different genitalia in both sexes. This problem, however, cannot be solved without much more material. Many of above-mentioned characters show that the genus has a close affinity to *Caenomyia* and related genera.

The species of this genus, which is confined to Tasmania and Australia, are distinguished as follows:

KEY TO SPECIES OF THE GENUS EXERETONEURA

1. Cross-vein between r_{2+3} (second longitudinal vein) and r_4 situated distinctly apicad of the apex of r_1. Basal part of r_4 between the common stem with r_5 and the above-mentioned cross-vein directed slightly apicad or at most perpendicular to the anterior margin of wing. Alula absent with a straight hind margin (♂) or quite rudimentary, with nearly straight hind margin (♀). The frons at level of the base of antennae in both sexes a little broader than the horizontal diameter of the eye. Vertex about equal to ¼ head width in both sexes. Third antennal joint comparatively broad and short, a little longer than the 2 basal joints together. Wings with 2 sharply marked dark spots. Halteres darkened. Tasmania, New South Wales ..... *E. maculipennis* Macq. ♂, ♀

The above-mentioned cross-vein situated distinctly basad of the apex of r_1. Basal part of r_4 directed slightly or very distinctly towards the base of wing. Alula always present, moderately developed, with a rounded hind margin. The frons on the level of base of antennae in both sexes nearly ⅓ as long as the horizontal diameter of the eye. Vertex in both sexes at least 1/7 of the head width. Third antennal joint narrow, long, nearly twice as long as the 2 basal joints together. Wings without well-marked spots or only the tip evenly darkened. Halteres yellow 2

2 (1). Hairs on tergites predominantly yellowish red. New South Wales ..... *E. zentae*, sp. nov. ♂

Hairs on tergites predominantly black 3

3 (2). Ocellar triangle and frons invisible when head viewed in profile, or at most only the anterior ocellus visible. The sides of the frons converge slightly towards a point well before the anterior ocellus and then suddenly diverge again towards the base of antennae. Width of the frons at level of anterior ocellus less than distance between outer sides of basal antennal joints. New South Wales, Tasmania ..... *E. angustifrons* Hardy ♂, ♀

Ocellar triangle and the upper part of frons clearly visible when head viewed in profile. Sides of frons diverge slightly towards a point just in front of anterior ocellus, and then diverge even more than previously. Width of the frons at level of anterior ocellus distinctly greater than distance between outer sides of basal antennal joints. Victoria, New South Wales ..... *E. tertia*, sp. nov. ♂, ♀

EXERETONEURA TERTIA, sp. nov. ♂, ♀

The most important characters of this species have already been mentioned in the key.

Proboscis extremely short, but labella long, fleshy, occupying whole mouth cavity; palpi a little shorter than labella. Parafacialia yellow-haired. Basal part of 3rd antennal joint very short, occupying about ¼ of its length (in *E. maculipennis* a little less than ½). Vertex broader than the total width of the ocellar triangle and the 2 ocelli (in *E. angustifrons* it is equal to the width of ocellar triangle and in *E. maculipennis* 3 times as broad). Ocellar triangle mostly black-haired, area at base of antennae mostly yellow-haired (in *E. angustifrons* they are brighter).

Mesonotum with greyish dust and 3 very narrow brown longitudinal stripes; hairs not very long and dense, black and yellowish, the under side of thorax densely yellowish-haired.

Wings greyish, little yellowish in parts; the 2 well-marked dark spots, present in *E. maculipennis*, are absent; the apical part of wing a little darker than the basal part, but the boundary between these areas not so well marked as in *E. angustifrons*.

The upper side of abdomen is very rubbed in 2 females, but it appears that the hind margins of the tergites are not so distinctly whitish-haired as in *E. maculipennis*, and have no median and lateral whitish-haired spots, which are present in *E. angustifrons*. The male has very well-marked narrow, yellowish-haired bands on the hind margins of tergites.

Length of body 13-16 mm., of wing 14-17 mm.

1 ♀, Jan. 1921, Millgrove, Vic. (F. E. Wilson); 1 ♀, Bright, Vic. (H. W. Davies); 1 ♀, 3.ii.1946, Tin Mine Huts, Kosciusko, 4100 ft. (K. C. McKeown); 1 ♀, Mallee, Vic. The type female in Division of Entomology Museum, C.S.I.R.O., Canberra.

Exeretoneura angustifrons Hardy ♂, ♀

Exeretoneura angustifrons Hardy, 1924, Proc. Linn. Soc. N.S.W. 49 (4): 458.

The author has seen specimens from the following localities: 1 ♂, 2.iii.1948, Bendora, A.C.T. (S. J. Paramonov); 1 ♂, 19.ii.1938, Lee's Springs, A.C.T. (T. G. Campbell); 2 ♂♂, 13.ii.1950, Lee's Springs, A.C.T. (S. J. Paramonov); 2 ♂♂, 23, 30.i.1946, Callista, Vic., 5,000 ft. (A. Burns). A mountain form occurring at altitudes greater than 3,500 ft.

Exeretoneura maculipennis Macquart ♂, ♀

Exeretoneura maculipennis Macquart, 1846, Dipt. Exot. Suppl. 1: 106.

The author has seen specimens from the following localities: 1 ♂, 9.ii.1946, Hotel Kosciusko, N.S.W., 5,440 ft. (K. C. McKeown); 1 ♂, 2 ♀♀, 28.i.1946, the Chalet, Mt. Kosciusko, N.S.W., 5,740 ft. (K. C. McKeown); 1 ♀, 12.i.1948, Upper Manning River, N.S.W., 4,200 ft. (A. Musgrave); 1 ♂, 24.i.1928, Interlaken, Tas. (A. Musgrave); 1 ♂, 1.ii.1949, between Cradle and Miena, Tas. (E. F. Riek); 1 ♂, 25.i.1949, Lake St. Clair, Tas. (E. F. Riek); 1 ♂, 30.i.1948, near Bronte, Tas. (Key, Carne, and Kerr); 1 ♀, 27.i.1949, Miena, Tas. (E. F. Riek).

Exeretoneura zentae, sp. nov. ♂

Distinguished from *E. maculipennis* by uniform colour of wing and very narrow frontal stripe; from *E. angustifrons* and *E. tertia* by position of the vein separating upper basal cell from the discal cell: it touches the vein m_3 ("diagonal" vein, running into hind margin of wing) at a point near the middle of the central portion of vein m_3; in *E. angustifrons* and *E. tertia* it touches m_3 at a point about ¾ of the way along its central portion.

Superficially very similar to *E. angustifrons*, but apart from above difference distinguished at once by (1) broader frontal stripe, occupying $\frac{1}{7}$ of the head

width (in *E. angustifrons* $\frac{1}{9}$ of it); (2) frontal stripe midway between base of antennae and ocellar triangle sunken (not flat as in *E. angustifrons*); (3) much shorter ocellar triangle (the distance between anterior and posterior ocelli is at most 1.5 times more than it is between the posterior ocelli; in *E. angustifrons* it is at least twice more); (4) shortened basal 2 antennal joints, which are together at most $\frac{1}{3}$ the length of the 3rd joint (in *E. angustifrons* only $\frac{1}{2}$); (5) 3rd antennal joint is comparatively broader, and not as slender as in *E. angustifrons*; (6) absence of the 1 very acute small tubercle (as spine) at apex of 3rd joint, which is always present in *E. angustifrons*; (7) presence of 1 additional veinlet at basal part of r_4, directed towards the base of wing; (8) wing quite uniform-coloured (in *E. angustifrons* it has traces of slightly more darkened areas); (9) hind and middle femora dark (in *E. angustifrons* yellow); (10) at hind margin of 2nd, 3rd, 4th, and (in part) 5th tergites there is a very narrow, nearly uninterrupted, smoky-white crossband, which in *E. angustifrons* is distinctly interrupted and is represented only by 3 spots: 1 central and 2 lateral; (11) tergites, with exception of the 1st, are densely covered by golden-reddish appressed hairs (in *E. angustifrons* they are black).

Most of the above-mentioned characters also serve to distinguish this species from *E. tertia*. However, *E. tertia* also differs from it by (1) the very highly situated, swollen frontal stripe and (2) the oblique direction (in relation to the long axis) of the basal part of vein r_4 and the additional cross-vein, the 2 being almost in a straight line.

Length of body 16 mm., of wing 13 mm.

1 ♂, 27.ii.1953, near Braidwood, N.S.W. (Miss Zenta Liepa).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

4. Genus ATRIADOPS Wandolleck

Atriadops Wandolleck, 1897, Ent. Nachricht. **23** (16): 241.

Hitherto authorities such as Bequaert (1935) and Mackerras (1925) recognized only 1 widely distributed species of this genus, *A. javana*.

Among available material the author has discovered a new species from Aru I. which differs clearly from *A. javana* by its nearly evenly darkened wings (including the basal part), and by the structure of the frons etc.; moreover there is evidence that 2 forms (?) of *A. javana* occur.

Key to Species of the Genus Atriadops

1. A large species, length of wing 16.6 mm. Eyes completely conjoined for some distance. Ocellar triangle extremely narrow and short, rudimentary. Wing dark in colour, with a few almost invisible pale spots, which are much more distinct in *A. javana*. Abdomen extremely broad, much broader than the wing at widest point. Aru I. ..... *A. aruana*, sp. nov. ♂

   Smaller species, length of wing to 14 mm., usually 11 mm. Eyes conjoined only at 1 point or separated for some distance. Ocellar triangle small but clearly visible. Wings variable in colour, sharply marked paler spots always present. Abdomen distinctly broader than thorax, but only a little broader than the wing. 2

2 (1). Basal part of axillary cell as well as the other light spots of wing milky-white . . . . *A. javana* Wied. ♂, ♀

Basal part of axillary cell dark, the other spots dark grey or brownish, only a little paler than the remainder of wing surface . . . . . *A. westwoodi* Lichtw. ♂, ♀

Atriadops aruana, sp. nov. ♂

Ground colour of body dark brown, of the eyes nearly black. Head comparatively higher than in other forms, only a little broader than high (in other forms much broader). Face comparatively very narrow, viewed from front distinctly smaller (below, at broadest point) than the horizontal diameter of eye (in other forms distinctly broader).

Hairs on face and frons brownish. Facets very large, at least twice as large as in other forms; the difference in the size of the facets in upper $\frac{2}{3}$ and in lower $\frac{1}{3}$ is sharp; the smallest facets are as large as the large facets of other forms.

Ocellar triangle extremely narrow, rudimentary; eyes conjoined for a distance equal to twice the length of the ocellar triangle, or equal to ½ of the frons.

Thorax comparatively broad, only slightly longer than broad, whereas in other forms the thorax is distinctly longer than broad. Wings dark, but without hyaline, milky, or subhyaline spots, with only some spots slightly paler than ground colour. Cells between the "diagonal" vein and *Cu* uniformly brown, without any trace of spots; supernumerary veins along hind border absent.

Abdomen very broad, distinctly broader than thorax, and about twice as broad as head.

1 ♂, 1911, Aru I. (W. W. Froggatt).

The type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Atriadops javana Wiedemann ♂, ♀

Atriadops javana Wiedemann, 1824, Analecta Ent. 18 (2).

The synonymy of this species is complicated: after the publication of *A. javana* Wied. 1824, Westwood described *A. variegata*, in 1848, which Lichtwardt and other authors regarded as a synonym of *A. javana*. In 1909 Lichtwardt described *A. westwoodi*, but Mackerras and Bequaert regarded this species also as a synonym of *A. javana*. It seems probable that *A. westwoodi* is merely a form of *A. javana*, but the material available to the author is not sufficiently well preserved to allow of a definite decision.

The author has seen specimens from the following localities: 1 ♂, 24.vi.1933, Hector's Camp, Mary River, Northern Territory (T. G. Campbell); 1 ♂, 8.ii.1920, Clermont, Queensland; 1 ♂, Nambour, Queensland; 1 ♂, 15.xi.1916, Brisbane, Queensland (H. Hacker); 1 ♂, May 1925, Great Palm I., Queensland (G. H. Hardy); 1 ♂, 3.iv.1928, Cape York, Queensland (W. B. Barnard); 1 ♂, 15. 1928, Rockhampton, Queensland (F. Roberts).

Atriadops westwoodi Lichtwardt ♂, ♀

Atriadops westwoodi Lichtwardt, 1909, Dtsch. ent. Z., p. 649.

1 ♂, Dec. 1925, Brisbane, Queensland (G. H. Hardy); 1 ♂, Eidsvold, Queensland; 1 ♂, 4.xii.1920, Toowoomba, Queensland (G. H. Hardy); 1 ♂, June, 1917, Cairns, Queensland; 1 ♀, Townsville, Queensland (F. H. Taylor); 1 ♂, 5.v.1933, Dalby, Queensland; 1 ♀, June 1944, Ducklo, Queensland; 1 ♀, May 1934, Masthead I., Queensland; 1 ♂, 14.iv.1925, "Mooni, Cotts Hg."

The female is readily distinguished from the male by its separated eyes, by its long ovipositor, and by a narrow, long, and (on hind border) regularly rounded axillary cell; in male it is twice as broad, and equal to the breadth of the 2 basal cells together; in female it is equal to the breadth of only 1 of these cells.

From *A. javana* this form can be distinguished by the dark hind border of the wing, not contrasting noticeably with the remaining dark surface.

Lichtwardt's description is as follows: ♂. In der "Insecta Saunders.", Dipt. Tab. V. fig. 4a-c gibt Walker die Zeichnung eines Colax ohne Beschreibung. In der Tafel ist das Tier als *javanus* ? Wied. Auss. Zweifl. II.261.2 bezeichnet. Wiedemans Beschreibung "fast wasserklarer Innenrand der Flügel" kann aber unmöglich auf die gleichmässig schattierten Flügel des des Bildes bezogen werden. Mir liegt nur in der Sammlung Hermann-Erlangen ein ziemlich grosses ♂ aus Neuguinea vor, welches gleichmässig braun gefärbte Flügel hat. Dieses passt genau zu der Zeichnung, welche von Westwoods Hand geliefert ist. Seine *variegata* ist in die Synonyme gerückt; so moge diese Art ihren Namen als Erinnerung an den farbenfrohen Maler und Entomologen tragen.

Die Farbe des Tieres ist besonders am Hinterleibe mehr rotbraun. Die Behaarung der Brust und der Thoraxseiten, sowie hinter dem Schildchen kann hellbraun genannt werden. Die gleichmässig braunen Flügel zeigen ausser der kleinen, halbmondförmigen, weissen Zeichnung im Innenwinkel zwischen Costa und Radius 4 + 5 undeutliche dunkelbraune Fleckung, welche die Analader umsäumt, sich um die Schnittpunkt von Media und Cubitus in der Flügelmitte lagert und drei kleine Punkte bildet, welche am Flügelhinterrande zwischen den Mündungen von Cu_2 und $Cu_1 + M_3$ liegen. Die kurzen Beine sind braun mit wenig helleren Schienen und Tarsen. Es ist auffallend, dass alle mir vorliegenden Tiere an den Flügeln lädiert sind.

Körper 12 mm. lang, 5 mm. breit; Flügel 10 mm.

5. Genus TRICHOPSIDEA Westwood

Trichopsidea Westwood, 1839, Trans. Ent. Soc. Lond. 2: 151.

As Bequaert (1934) regarded the genera *Dicrotrypana* Big., *Symmictus* Loew., and *Parasymmictus* Big. only as synonyms of *Trichopsidea*, this genus is not only Australian, but very widely distributed. Only 1 Australian species, *T. oestracea* Westw., is known.

TRICHOPSIDEA OESTRACEA Westwood. ♂, ♀

Trichopsidea oestracea Westwood, 1839, Trans. Ent. Soc. Lond. **2**: 151.

The author has seen specimens from the following localities: 1 ♂, 5.xii.1947, Canberra, A.C.T. (E. F. Riek); 1 ♂, Dec. 1929, Red Hill, Canberra, A.C.T. (Tillyard); 1 ♂, 1.xii.1929, Brindabella, A.C.T. (Mackerras); 1 ♂, 20.xi.1931, Canberra, A.C.T. (L. F. Graham); 1 ♀, 17.xi.1941, Canberra, A.C.T. (S. H. Shepherd); and some other specimens bred from living grasshoppers, in Canberra; 1 ♀, 5.ii.1935, Hay, N.S.W., "bred from living grasshopper" (N. S. Noble); 1 ♂, 3.xii.1946, Blackheath, N.S.W. (A. Burns); 6 ♂♂, 1 ♀, 6-9.x.1947, Rannes, central Queensland (K. R. Norris); 1 ♀, Dec. 1922, Eidsvold, Queensland, 2 ♀♀, 1, 6.xii.1935, Dalby, Queensland (N. Geary); 4 ♀♀, 26.iii.1945, Mt. Larcom, Queensland (T. H. Smith), one with another label: "Parasite of *Prosoplus woodlackiana*."

6. Genus CYCLOPSIDEA Mackerras

Cyclopsidea Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50**: 557.

This extremely interesting genus was described only in 1925. As Mackerras gives a detailed description of this genus, it is omitted.

CYCLOPSIDEA HARDYI Mackerras ♂, ♀ (new)

Cyclopsidea hardyi Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50**: 557.

The author has seen specimens from the following localities: 1 ♂, 1 ♀, 2.i.1926, Galston, near Hornsby, N.S.W. (Wood); 1 ♂, 4.xii.1940, Nedlands, W.A. (K. R. Norris); 1 ♀, 14.i.1936, Kelmscott, W.A. (K. R. Norris); 1 ♂, 1 ♀, 1.i.1886, Hack's Bridge, ? S.A. (Tepper); 1 ♀, Cunnamulla, Queensland (N. Geary).

According to information from Mr. G. H. Hardy the type is lost; only a mount of the genitalia of the type is preserved.

Female (new).—Female differs from male only by its slightly broader vertex and its genitalia, which are very similar to those of *Trichophthalma*.

All specimens in the author's possession have the lower basal cell broader than in Figure 17 of Mackerras. The axillary cell is also as a rule broader than the anal cell, and has the hind margin rounded; the axillary cell of the female is more similar in form to Mackerras's figure. This species is so poorly represented in collections that it is impossible to determine the range of variation.

7. Genus HIRMONEURA Meigen

Hirmoneura, Meigen, 1820, Syst. Beschr. **2**: 132.

This genus was discussed by Bequaert (1932) but the author cannot agree with his subdivisions, which are quite artificial.

Hirmoneura ales Newman

Hirmoneura ales Newman, 1841.

Rhopaloceraeschata ales Newman, 1841. The Entomologist 1: 220 (no sex given), presumably from "New Holland."

Rhynchocerochata ales Kertesz, 1909. Cat. Dipt., vol. 4, p. 50.

Trichoisthalma ales Lichtwardt, 1910. Dtsch. ent. Z., p. 375. Hardy, 1934. Proc. Linn. Soc. N.S.W. 49 (4): 452; Mackerras, 1925, loc. cit., p. 510?

The description by Bequaert is quoted in extenso below:

"The v. Roeder Collection contains a male which is unquestionably the type of *R. ales*, labelled apparently in Newman's handwriting.

"This species has been a puzzle thus far, since the description was altogether too crude for recognition. It has generally been sought among the Australian Trichophthalmae: but the type shows at once that it could not possibly belong in that genus. The eyes are entirely bare and there is no indication that they ever were pilose. Moreover, the only wing left is very long and narrow, a feature which I have never seen in a species of *Trichophthalma*. Newman stated that "instrumenta cibaria desunt," and the authors have assumed that the long proboscis was accidentally broken off. But a careful examination of the specimen has convinced me that the proboscis was short and soft in the living insect: only the labella really are missing. In addition the shape of the face is like that of the subfamily *Hirmoneurinae*, not as in *Nemestrininae*. What is left of the proboscis is drawn back in a deep and narrow sinus of the lower part of the face; the face itself is not in the least swollen, the area between the base of the proboscis and antennae being completely flat: the sides of the face are grooved along the inner orbits, and the long and slender palpi may lie in these grooves; the palpi are distinctly three-segmented.

"Keeping in mind the possibility that the locality "New Holland" might have been erroneous, I have attempted to refer this insect to one of the described species of *Hirmoneura*.

"The absence of a cross-vein between the second longitudinal and the upper branch of the third, the absence of accessory cross-veins in the first and second posterior cells, as well as holoptic and bare eyes, place it in my subgenus *Hirmoneuropsis*. Only two of the described species appear to belong in that group, viz. *H. brevirostrata* Bigot (of Chile) and *H. basalis* Lichtwardt (of India). *H. brevirostrata*, which I have seen, is very different. *H. basalis* is described as having on the abdomen the first tergite and the basal half of the second ivory-white, the remainder of the dorsum of the abdomen being cinnamon brown. No such contrast of colour is seen in the type of *H. ales*, which has the dorsum of the abdomen uniformly dull, dark brown, with the shorter pilosity black and some greyish white longer pile toward the base and along the sides; ventrally the abdomen is covered mostly with appressed, yellowish white, somewhat silky hairs. The hind legs are entirely pale reddish yellow, the tibiae and tarsi being slender, and the tibiae not fringed. The wing has a very large alula and is 9 mm. long by 4.7 mm. wide: it is smoky throughout, but more infuscate toward the anterior margin and the base.

"I am inclined to regard this insect as a true Australian species of *Hirmoneura*, even though in recent years no member of that genus has been reported from Australia. Most probably it has escaped detection. I have, moreover, seen another, quite distinct and evidently undescribed species of *Hirmoneura* from Queensland."

8. Genus TRICHOPHTHALMA Westwood

Trichophthalma Westwood, 1835, Phil. Mag. **6**: 448.

This genus is extremely rich in Australia. Mackerras in 1925 mentioned 30 species, and the author has listed 45 species in this paper. Doubtless there are numerous as yet undescribed species in Australia. Edwards (1930) sinks the Chilean *Eurygastromyia* Lichtw. as a synonym to this genus.

Some species, for example *T. punctata* Macq., occur in enormous numbers. On a hot day in January the constant humming sound produced by hundreds of males hovering in the shade of eucalypt trees can be often heard. Unfortunately the life history of these species is unknown. They could be an important feature of a natural fauna.

It is noteworthy to add that the palpi are not 2-, but 3-jointed. Careful study has shown a basal, short joint to which is adjoined (not apically, but subapically) the so-called 1st joint of palpi.

Key to Australian Species of the Genus Trichophthalma

1. The short veinlet m_{3-4} (i.e. apical part of so-called "diagonal" vein) absent, and thus veins are not present in the hind margin of wing between the apex and the apex of anal cell (if this veinlet is present only on 1 wing, see below, point 3). A greyish species, very similar to *T. primitiva*, but smaller, with the alula at base triangular; female with a row of black median spots on abdomen which in *T. primitiva* are absent. Western Australia . . *T. grisea* Macker. ♂, ♀

   The veinlet m_{3-4} always present and as a rule represents the continuation of diagonal vein, but if not quite in the same straight line, the deviation is slight. Third joint of antennae round at base, without any trace of transverse sulcus. Face almost bare, or the hairs are not numerous and not masking the ground colour of the face 13

   The veinlet m_{3-4} situated not in the same straight line as the remainder of diagonal vein, but considerably more basal, the distance from the straight line being greater than length of the veinlet itself. Third antennal joint narrowed at base, having a well-marked sulcus (furrow) around. Face covered with very dense, long hairs, masking the ground colour (*T. bivittata* group) 2

2 (1). Ground colour of abdomen uniformly dark, but the hairs on hind margin of the tergites form narrow, yellowish, transverse bands or there are transverse alternate bands of greyish and dark hairs on whole surface of tergites (in 1 species, *T. grisea*, specimens with abnormal venation have a dark median stripe on the middle of tergites in the female) 3

   Ground colour of abdomen with 2 longitudinal rows of large greyish spots 6

3 (2). Venation abnormal: the veinlet m_{3-4} is only present on 1 wing . . . . . *T. grisea* Macker. ♂, ♀

   Venation normal 4

4 (3). On greyish ground of mesonotum there are small dark brown spots which form a kind of irregular longitudinal stripes. Abdomen with long and dense hairs forming transverse alternate bands. Whole body in general appearance grey. New South Wales, Queensland..... *T. primitiva* Walk. ♂, ♀

The dark brown or nearly black ground of mesonotum with 2 narrow, very clearly defined, light, submedian stripes, converging towards the scutellum. Hind margin of 2nd and 3rd tergites always covered with dense, shining, yellow, nearly golden hairs which form narrow transverse bands.....5

5 (4). Ground colour of scutellum uniformly dark. The length of wing at most 11 mm. Transverse bands on 2nd and 3rd tergites less developed, whitish. Frontal triangle in male nearly equilateral. Frons in female diverging from the ocellar triangle. South Australia, New South Wales ....*T. ricardoae* Lichtw. ♂, ♀

Ground colour of scutellum always with a triangular paler spot at base. Length of wing at least 12.5 mm. Transverse bands on 2nd and 3rd tergites more developed, golden. Frontal triangle in male very narrow, high; in female the sides of frons are parallel for a distance equal to length of ocellar triangle and then diverge. Victoria, New South Wales.....*T. laetilinea* Walk. ♂, ♀

6 (2). Abdomen black, with yellow spots; the sides of abdomen with tufts of yellow and black hairs. South Australia. Female unknown.....*T. variolosa* Lichtw. ♂

Abdomen black, with greyish, bluish, but not yellow spots 7

7 (6). Mesonotum dark brown, with 2 sharply marked narrow, submedian light stripes, which converge slightly towards the scutellum and extend from the anterior border to the scutellum. Scutellum uniformly coloured..... 8

Mesonotum greyish blue, with a dark narrow median stripe, which is broader towards the scutellum, and with 2 less marked, abbreviated black lateral stripes, which are often absent or separated into 2-3 spots. The dark median stripe becomes broader and extends over scutellum and abdomen, forming a single median stripe from the anterior border of scutellum to the apex of abdomen. Scutellum with a dark median stripe.....9

8 (7). Eyes completely contiguous (in male). A smaller and more brownish species with distinctly denser hairs on whole body. The vein at apex of discal cell very short. Cross-vein *r-m* point-like. Alula at base triangular, acute, but hind margin straight. Tarsi yellow, only at apex a little darker. New South Wales, Queensland..... *T. albimacula* Walk. ♂, ♀

Similar to the typical form, but differs by the presence of small yellow-reddish spots of ground colour at anterior corners laterally on the 2nd, 3rd, and 4th tergites. Western Australia.... .. *T. albimacula occidentalis,* subsp. nov.

Eyes in male not completely contiguous, but separated by a very narrow stripe, and nearly touching only at 1 point. A larger, greyish species, with less dense hairs. Cross-vein *r-m* (at apex of upper basal cell in longitudinal position) long. The vein at apex of discal cell also long. Alula at base triangular, acute, but hind margin distinctly concave. Tarsi dark. White hairs on sides of mesonotum and scutellum very well marked. New South Wales ....
T. waterhousei, sp. nov. ♂, ♀

Eyes as in *T. albimacula,* smaller than the last species, but of same brownish appearance. Venation, form of alula, and tarsi as in *T. waterhousei.* New South Wales (Sydney).... ... .*T. thomsoni,* sp. nov. ♂

9 (7). Alula extremely developed in direction perpendicular to the long axis of wing; at broadest point its width is greater than distance between the point at which it touches the axillary cell and the anterior margin of wing (in area of humeral vein). Head in male not almost hemispherical, or very convex in female (viewed from above), but distinctly flattened. Eyes in male separated by a stripe which is a little narrower than the anterior ocellus; the narrow space as long as ocellar triangle. Western Australia.....*T. alulata,* sp. nov. ♂, ♀

Alula distinctly longer than broad. At broadest point it is shorter than the distance from the point at which it touches the axillary cell to the anterior margin of wing. Eyes in male completely contiguous over a distance much greater than the length of the ocellar triangle 10

10 (9). Under side of body in male is distinctly rose-haired, in female whitish-haired, but the sides of the segments near ovipositor, the palpi, and some other parts also rose-haired. The submedian dark markings on the anterior part of mesonotum are as a rule poorly developed. New South Wales, Queensland.....
T. rosea Macq. ♂, ♀

Under side of the whole body is whitish- or yellowish-haired.....11

11 (10). The hairs which in male cover the black median and 2 submedian yellowish stripes on abdomen are very dense, long, reclining, and mask the ground colour of body. Black median stripe of abdomen in both sexes always with straight sides. Third joint of antennae brownish, not bright orange. Black hairs on frons and face numerous and clearly visible. Frons in female distinctly broader on level of anterior ocellus than the proboscis at its base. Western Australia.....
T. bivittata wheeleri Beq. ♂, ♀

The above-mentioned hairs in male are erect, not very dense, and do not mask the dark and yellowish ground of the above-mentioned stripes. Black median stripe of abdomen as a rule with jagged outer margins. Third antennal joint bright orange. Black hairs on frons and face in male not clearly visible. Frons of female on the level of anterior ocellus narrower than the base of proboscis or at most as broad as it 12

12 (11). Two submedian longitudinal stripes of upper side of abdomen and the 2 submedian stripes on mesonotum distinctly yellowish grey. Length of body as a rule more than 18 mm. A typical, usual form. New South Wales, Queensland..
T. bivittata bivittata Westw. (= *eques* Schin.) ♂, ♀

All above-mentioned stripes bluish grey. Size smaller—15 mm. New South Wales
T. bivittata Westw. forma *coerulea* nov. ♂, ♀

13 (6). Face bare, in profile only slightly protruding; its sides are nearly parallel to the margin of eyes and at lowest point are as broad as or 1.5 times as broad as the 1st antennal joint. Apex of face situated very high, much nearer to base of antennae than to base of palpi. Ocellar triangle twice as long as broad. Third antennal joint onion-shaped. The middle lower genital plate in male extremely long and narrow. Palpi comparatively thick, swollen.....14

Face at sides as a rule haired, in profile rather protruding; its sides are not parallel to the margin of eye; at lowest point 2-4 times as broad as the 1st antennal joint. Apex of face situated comparatively far from the base of antennae. Ocellar triangle only slightly elongated. Third antennal joint conical, elongated. The middle lower genital plate in male usually triangular, or if parallel-sided broad, nearly as broad as the lateral plates. Palpi thin, not swollen..... 19

14 (13). Abdomen with a very sharply marked, broad, black, median, longitudinal stripe, and with 2 yellowish grey, also nearly parallel-sided stripes beside the median stripe; moreover, there are 2 similar broad and clearly defined black lateral stripes. Frons in male yellow-haired, in female only on the lower ¼. Joints of the front and middle tarsi (particularly the penultimate) distinctly dilated, broader than metatarsus. Antennae, palpi, legs, halteres, face, frons, and scutellum yellow. Length of body 14-19 mm. New South Wales, Queensland..... *T. nigrovittata* Macker. ♂, ♀

Abdomen without 5 very sharply marked longitudinal stripes.....15

15 (14). Legs and halteres wholly yellow or reddish. Veins reddish. Sides of mesothorax covered with yellowish or greyish hairs, not bright and not contrasting with the ground colour. Anterior and middle tarsi dilated or normal.....16

At least the hind femora and tarsi black. Halteres brownish. Veins brown. Sides of mesonotum covered with bright sulphur-yellow hairs, which contrast markedly with the dark ground colour of mesonotum, which has a bluish nuance.....18

16 (15). Wings nearly hyaline, greyish; alula at base rounded. Scutellum black, with dense grey dusting. All tarsal joints equally broad. Mesonotum black, with grey dusting. Frontal stripe on upper side of male a little broader than the anterior ocellus. Third joint of antennae nearly onion-shaped. Abdomen reddish with narrow dark median stripe in male and with a very broad one in female. Queensland.....*T. bancrofti* Macker. ♂, ♀

Wings, alula, and tarsi as in *T. bancrofti*. Scutellum brown. Mesonotum more brown than in *T. novaehollandiae*. Third joint of antennae as in *T. bancrofti*. Abdomen dark brown, partly brown-reddish, in general appearance as in *T. novaehollandiae*. The touching line of eyes very long, equal in length to ½ the distance between the anterior ocellus and base of antennae. Head viewed from above very convex, nearly hemispherical (in *T. bancrofti* distinctly flattened). Face narrower than in *T. bancrofti*, at base equal in width to ½ the horizontal diameter of eye. Queensland..... *T. froggatti*, sp. nov. ♂

Whole surface of wing distinctly yellowish or yellowish-brown suffused. Mesonotum and abdomen brown, in some places (here and there) reddish. Scutellum reddish. The 2nd, 3rd, and 4th tarsal joints are more or less dilated, the 4th being always broader at apex than the 2nd.....17

17 (16). Alula at base rounded. Wings extremely long. Frontal stripe in male as broad as anterior ocellus. Fourth joint of anterior and middle tarsi broader than the 2nd, subacute on both sides. As a rule larger than the following species. Queensland..... *T. doddi*, sp. nov. ♂, ♀

Alula at base acute, triangular. Wings of normal length. Eyes in male touching for a considerable distance. Fourth joint of anterior and middle tarsi distinctly broader than the 2nd and on outer side it bears an acute prolongation distinctly longer than that on the inner side. South Australia, Victoria, New South Wales, Queensland.....*T. novaehollandiae* Macq. ♂, ♀

18 (15). Ground colour of abdomen dark, with dull bluish nuance, as on mesonotum. All femora black, tarsi darkened. Colour of abdomen uniform, without darker bands on the basal part of tergites. Victoria, New South Wales, Queensland..... *T. scapularis* Big. (= *nigripes* Macq.) ♂, ♀

Ground colour of abdomen reddish, with a bluish, nearly purple nuance. Anterior and middle legs, hind femora mostly yellow or reddish. Second, 3rd, and 4th tergites viewed from the side have the anterior part darker than the posterior.

This form lives in coastal area of the northern part of eastern Australia.....
T. scapularis Big. var. *pallipes,* var. nov. ♂, ♀

19 (13). Males (eyes contiguous or separated by an extremely narrow stripe).....20
Females (eyes always separated by a stripe at least as broad as the ocellar triangle).....46

20 (19). Ground colour of abdomen uniformly dark, without a darker median stripe; if there are dark spots on median line they are indistinct and never form a complete dark longitudinal stripe. The species of this group never have the sides of abdomen bright yellow or 1, 3, or 5 longitudinal stripes of different (mostly dark) colours; if the ground colour is reddish at sides, the spots are indistinct and the reddish colour is translucent.....21

Abdomen always with very well-marked narrow median dark stripe or (rarely) with a row of small spots (in this case the sides of abdomen are distinctly yellow, not reddish). Often the abdomen has 5 longitudinal stripes, viz. 2 lateral, 1 median (all dark), and 2 sublateral (paler), or abdomen has only 3 stripes; viz. 1 dark median and 2 lighter (mostly yellow) lateral, or it has only a median dark stripe and the remaining surface is yellowish or yellowish grey.....30

21 (20). Hind margin of the last tergite with a very characteristic incision in the middle (these are the only *Trichophthalma* species with this incision). Ground colour of body dark, without any traces of lateral or reddish spots.....22

Hind margin of the last tergite convex in the middle (where there is a small tubercle), or if it is concave, the concavity is very broad, and rounded in form. Ground colour of abdomen at sides predominantly reddish or yellow; only *T. fullerae* and *T. mackerrasi,* spp. nov. have the ground colour dark.....23

22 (21). Lobes of the hind margin of last tergite viewed from above are nearly quadrangular, the incision in the middle being deep, sharp, and narrow (Fig. 5*A*). Alula at base triangular, acute. There are black hairs at sides of thorax. Sides of abdomen with dark spots, but not with complete, very narrow, and regular longitudinal dark stripes. Queensland, New South Wales.....
T. fusca Macker. ♂, ♀

Lobes of the hind margin of last tergite viewed from above are rounded, not quadrangular, the incision in the middle being nearly as broad as the lateral lobes (Fig. 5*B*). Alula at base subacute, rounded, not distinctly triangular. Sides of mesonotum from the humeri towards the base of wings with dense, long, and strong black hairs. Sides of abdomen with longitudinal narrow and regular black stripe. South Australia ....*T. calabyi,* sp. nov. ♂

23 (21). Ground colour of abdomen dark, no reddish spots at sides of tergites, or they are only slightly visible. Base of alula in *T. fullerae,* sp. nov. rounded, subacute; in *T. mackerrasi,* sp. nov. acute, triangular.....24

Sides of abdomen as a rule broadly reddish (not bright). Base of alula always rounded, not acute, triangular 25

24 (23). Base of alula triangular, acute. Ocellar triangle elongated, distance between the anterior ocellus and the posterior pair is twice as great as that between the posterior ocelli .... *T. mackerrasi,* sp. nov. ♂

Base of alula rounded. Ocellar triangle only a little elongated.. .....
T. fullerae, sp. nov. ♂

25 (23). Base of abdomen with a very well-developed transverse band of pure white hairs..26

Base of abdomen without this band; if the hairs at base of abdomen are paler than the remainder, they are never pure white, but only yellowish or greyish.....27

26 (25). Apical ⅓ of wing clearly white, nearly milky white. Alula extremely broad, distinctly broader than the axillary lobe; only a little longer than broad. Western Australia.....*T. apicalis* Macker. ♂

Tip of wing without a white marking. Alula only a little broader than the axillary lobe, distinctly longer than broad. Eastern Australia....*T. costalis* Westw. ♂

27 (25). Keel on the upper part of frons convex as usual.....28
Keel divided by a median furrow, or nearly absent, being replaced by furrow ...29

28 (27). Ocellar triangle elongated, clearly not equilateral. Face bright brown. Abdomen without dark narrow band on the hind margins of the 2nd, 3rd, and 4th tergites, abdomen reddish with a narrow longitudinal dark stripe. Queensland....
T. intermedia Macker. ♂

Ocellar triangle nearly equilateral, only slightly elongated. Face black. Abdomen with a narrow dark band on the hind margin of the 2nd, 3rd, and 4th tergites. Queensland.....*T. transversa,* sp. nov. ♂

Ocellar triangle very elongated, nearly twice as long as broad. Face yellow. Abdomen mostly dark, with only narrow reddish area at sides. Western Australia.....*T. costalis soror,* subsp. nov. ♂

29 (27). Ocellar triangle nearly equilateral. Furrow between face and eyes very narrow, indistinct. Thorax uniformly yellowish-dusted. Western Australia.....
T. subcostalis Macker. ♂

Ocellar triangle elongated. Furrow between face and eyes very clearly visible, as broad as the palpi. On thorax there are as a rule 2 small whitish spots. New South Wales.....*T. rufonigra* Macker. ♂

30 (20). Abdomen always with at least 3 dark longitudinal stripes (1 median, 2 lateral); the lateral stripes are sometimes broken up into spots, but their longitudinal disposition is preserved.....31

Abdomen always without 3 distinct dark longitudinal stripes, only the median being represented, and often broken up into isolated dark spots. If there are dark spots at sides of abdomen they are poorly developed and never have the form of a longitudinal stripe. Abdomen predominantly yellow in most species..40

31 (30). Alula at base distinctly rounded (in female also), its width being at least as broad as distance from its apical point to the apex of humeral vein. Mesonotum with 3 dark and 4 greyish longitudinal stripes of nearly equal width, viz. 1 dark median, 2 greyish submedian, 2 dark sublateral, and 2 greyish lateral. New South Wales.....*T. confusa* Macker. ♂

Alula narrow, triangular, at base acute.....32

32 (31). Scutellum ferruginous.....33
Scutellum dark brown or nearly black.....34

33 (32). Greyish white longitudinal stripes on mesonotum very narrow, sharply marked, ½ as broad as the brown median stripe. The similar stripes on abdomen are also nearly ½ as broad as the median brown stripe; the hairs on these stripes are sparse and mostly black, erect. Frons below the anterior ocellus distinctly broader than ocellus, the white hairs distributed in 3 tufts: one a little below

the anterior ocellus and 2 above the base of antennae, the hairs of the latter procumbent. Apical ½ of palpi with short but strong black hairs. Face not shining. Anterior part of wing a little darkened, but the boundary very indistinct. This species is readily distinguished by the 5 clearly defined longitudinal stripes on tergite. Western Australia.....*T. leucophaea* Walk. ♂

Greyish white longitudinal stripes on mesonotum broad, without clearly defined margins, as broad as the median brown stripe. The similar stripes on abdomen as broad as the median and lateral stripes, their margins very indistinct; there is a mixture on these stripes of black and yellow, dense, and rather long hairs. Frons below anterior ocellus as broad as ocellus. White hairs on the frons extremely sparse, short. Face mostly shining. Palpi with yellowish hairs. Nearly whole surface of wing suffused, on anterior margin more intensely, but there is no clearly marked boundary, the colour gradually diminishing towards the hind margin. Western Australia....*T. degener* Walk. (= *longirostris* Macker.)

34 (32). Submedian grey stripes of abdomen without a distinct yellow transparent nuance 35
Submedian grey stripes in tergites have a clearly visible yellow nuance.....36

35 (34). Similar to *T. leucophaea*, but the greyish longitudinal stripes on abdomen are broader, nearly equal to the median stripe; greyish stripes are nearly parallel-sided, whilst in *T. leucophaea* they have jagged edges. Wings with very narrow, sharply marked, dark pattern along the anterior border, the other surface hyaline. Face not shining. Palpi with yellow hairs. Frons distinctly narrower than the anterior ocellus, with hairs directed upwards. Western Australia.. .....
T. griseola, sp. nov. ♂

Similar to *T. degener* Walk. and particularly to *T. griseola*. Differs from *T. degener* by the coloration of the wing, which is similar to that of *T. griseola*, by the more densely haired frons, by the dull face, and by the more sharply marked greyish longitudinal stripes of abdomen, which are distinctly broader than the median brown stripe. Third antennal joint very long comparatively, conical, distinctly longer than 2 basal joints together (in *T. degener* Walk. it it pear-like, short, shorter than basal 2 joints together). Western Australia....
T. regina, sp. nov. ♂

36 (34). Sides of mesonotum with a broad longitudinal stripe of greyish dust, extending over postalar calli (the external part of these calli is always very well marked by grey dust).....37

Lateral greyish stripe on mesonotum poorly developed, never clearly visible on the postalar calli.....39

37 (36). Frons in the male without keel in upper ½, or it is sunken. Hind femora yellow, not darkened. On middle part of mesonotum no golden adpressed hairs. Mesonotum with 2 (in very well-preserved specimens 3) longitudinal, narrow, paler stripes, but they are not very well developed. New South Wales.....
T. nicholsoni Macker. ♂

Frons with a keel in the upper ½. Hind femora always darkened, at least on 2/3 of outer side. Mesonotum without median and 2 submedian stripes, but there are rather numerous golden adpressed hairs on middle line of mesonotum, especially in front of scutellum, and if mesonotum is striped, the face is covered with black hairs.....38

38 (37). Mesonotum striped, no golden adpressed hairs on middle line. Face clothed with black hairs. Victoria, New South Wales.....*T. dubiosa* Macker. ♂

Mesonotum not striped. On middle line of mesonotum, particularly in front of scutellum, there are golden adpressed hairs. Victoria, New South Wales, Queensland .. .. *T. bivitta* Walk. ♂

(*a*) Costa pale brown, very small species, 10 mm.... *T. bivitta* Walk. (typica)

(*b*) Costa very dark brown, species of medium size, 13 mm. ....
T. bivitta nigricosta Macker.

39 (36). Mesonotum without longitudinal stripes. Lateral stripes of abdomen well developed, as broad as the median, occupying 1/7 of the width of tergites (female unknown). Western Australia..... *T. ruficosta* Macker. ♂

Mesonotum with 2 rather broad longitudinal grey stripes. South Australia.....
T. griseolineata Macker. ♂

(Male of *T. trilinealis* unknown.)

40 (30). Mesonotum with 2 narrow, but very distinct paler stripes from the anterior margin to the scutellum, converging a little towards the scutellum. There are also 2 distinct paler lateral stripes.... 41

Mesonotum without distinct paler longitudinal stripes either in submedian or lateral areas..... 42

41 (40). Palpi and antennae black. Face black-haired. New South Wales, Victoria (female unknown)..... .....*T. lutea,* sp. nov. ♂

Palpi and antennae tawny. Face with yellow hairs. Western Australia (female unknown).....*T. fulva* Walk. ♂

42 (40). Alula very broad, rounded; at base always rounded.....43
Alula narrow, triangular, at base distinctly acute.....44

43. (42). Lower median genital plate extremely broad at base, broader than the lateral plates, and occupying nearly whole width of the genitalia; it is even at a joint half way between base a little broader than the lateral plates and apex; at apex it is broad, rounded. Apices of the lateral plates a little longer than the apex of the median plate. Sides of face as a rule with long and dense black hairs.....*T. orientalis* Macker. ♂

Lower median genital plate long, narrow, tongue-shaped, at base not broader than the lateral plates; it narrows towards the apex, but very slightly, and at apex is rather broad, nearly as broad as the lateral plates, rounded; its apex is situated on same level as the apices of the lateral plates. Boundaries between the median and lateral plates nearly straight, without excavations, the plates situated very close to one another. Face and sides with yellowish, not very long hairs.....*T. punctata* Macq. ♂

44 (42). Genitalia nearly as in *T. orientalis.* Palpi black, black-haired. Face mostly with dark hairs. Frontal stripe below the anterior ocellus narrower than the anterior ocellus, very long. Antennae dark, with basal joints short, nearly quadrangular. Mesonotum and tergites with sparse golden adpressed hairs. Many black, long, erect hairs on scutellum and tergites. Length of body 10 mm. New South Wales ..... *T. harrisoni* Macker. ♂

The genitalia nearly as in *T. punctata* (43). Palpi yellow, yellow-haired. Face also with only yellow hairs. Frontal stripe below the anterior ocellus broader than ocellus. Mesonotum and tergites without golden adpressed hairs.....45

45 (44). Wing along the costa only slightly darkened. Mesonotum without 2 very broad greyish stripes. Under side of thorax yellowish-haired, only slightly lighter than upper side. Western Australia.....*T. glauerti,* sp. nov. ♂

Wing along the costa narrowly, but intensely dark brown; mesonotum with 2 very broad greyish stripes. Under side of thorax whitish-haired, upper side yellow-haired. Western Australia ..... *T. fortei*, sp. nov. ♂

46 (19). Large species* (length of wing at least 18 mm.). No longitudinal stripes on mesonotum or on abdomen 47

Smaller species 48

47 (46). Sides of abdomen dark reddish, always lighter than the middle part of abdomen. hind tarsi nearly black. No greyish cross-bands on hind margin of 2nd and 3rd tergites ..... *T. rufonigra* Macker. ♀

Sides of abdomen of the same colour as the middle part. Hind tarsi reddish. Along the whole hind margin of 2nd and 3rd tergites there are greyish parallel-sided cross-bands ..... *T. apicalis* Macker. ♀

48 (46). First segment of abdomen and the basal part of the 2nd with white tomentum, and these parts as well as under side of scutellum with pure white dense hairs; these hairs form a clearly defined pure white cross-band at base of abdomen. Tarsi and tibiae much darker than femora. Upper side of abdomen uniformly brown ..... *T. costalis* Westw. ♀

No such white cross-band at base of abdomen 49

49 (48). Abdomen with 3 or 5 very distinct longitudinal stripes; very often mesonotum is also striped (2 lateral and 2 submedian stripes) 50

Abdomen without stripes or with indistinct stripes 55

50 (49). Abdomen with 5 very clearly defined longitudinal stripes (2 lateral and 1 median stripe are brown, 2 submedian grey). Proboscis unusually long. Western Australia ..... *T. leucophaea* Walk. ♀

Abdomen with only 3 longitudinal stripes; if there are also lateral stripes, these are always much narrower than the median. In *T. leucophaea* the lateral and median stripes are nearly of equal width 51

51 (50). Mesonotum with 2 broad and distinct brown sublateral stripes; sometimes the very broad, grey median area has a 3rd less distinct median brown stripe. No golden hairs on mesonotum. The dark median stripe on abdomen little smaller than the 2 grey submedian stripes ..... *T. confusa* Macker. ♀

Mesonotum black with 2 or 3 narrow greyish longitudinal stripes in the disc or without them; there are also 2 greyish lateral stripes, which are sometimes absent 52

52 (51). Mesonotum with some adpressed golden hairs under the usual hairs; similar hairs can occur also on the tergites 53

No golden adpressed hairs on mesonotum and abdomen 54

53 (52). The dark median stripe on abdomen very narrow, the yellowish grey submedian stripes extremely broad, occupying nearly whole surface of abdomen, the dark lateral stripes therefore nearly absent ..... *T. harrisoni* Macker. ♀

The dark median stripe of abdomen nearly equal to submedian stripes; the dark lateral stripes rather well developed ..... *T. bivitta bivitta* Walk. ♀ and *T. bivitta nigricosta* Macker. ♀

* The females of many *Trichophthalma* species are much more difficult to distinguish than the males. At present one can be sure of placing them only in their correct species-group. As the females of many species have not yet been described, an exact key for their identification must await more extensive collecting and study.

54 (52). Mesonotum at sides with a very faint indication of greyish white stripes, but with 3 narrow, very well-defined brown longitudinal lines . . . . *T. trilinealis* Macker. ♀

Mesonotum at sides with pale zone small and obscure, and with 2 greyish stripes broader than in *T. trilinealis* . . . . . *T. griseolineata* Macker. ♀

Mesonotum at sides with very well-marked and broad greyish white lateral stripes, in the disc with 2 narrow pale submedian longitudinal stripes . . . . . *T. nicholsoni* Macker. ♀

55 (49). A group of poorly studied species, very difficult to distinguish: (*T. fusca* Macker., *mackerrasi*, sp. nov., *intermedia* Macker., *degener* Walk., *fulva* Walk., *orientalis* Macker., *punctata* Macq., *dubiosa* Macker.) 56

The females of these species have not yet been described: (*T. ruficosta* Macker., *fortei*, sp. nov., *glauerti*, sp. nov., *transversa*, sp. nov., *calabyi*, sp. nov., *griseola*, sp. nov., *regina*, sp. nov., *subcostalis* Macker., *lutea*, sp. nov., *fullerae*, sp. nov., *fulva* Walk.).

56 (55). Mesonotum not striped (*T. fusca* Macker., *intermedia* Macker., *mackerrasi*, sp. nov., *punctata* Macq., *orientalis* Macker.).

Mesonotum striped (*T. degener* Walk. and *T. dubiosa* Macker.).

Description of Species

1. Trichophthalma rosea Macquart ♂, ♀

Macquart, 1846, Dipt. Exot. Suppl. **1**: 100.

The author has seen all the material from the various museums studied by Dr. Mackerras and can add only a few new localities and data: ♂♂, ♀♀, 20.viii.-6.ix, Stanthorpe, Queensland (H. Jarvis); 1 ♂, 1 ♀, 22.viii.1948 Kuringai, near Sydney, N.S.W. (S. J. Paramonov); 1 ♂, 17.viii.1947, Cowan, N.S.W. (Rodd); 1 ♂, Galston (Dumbrell); 4 ♂♂, 2 ♀♀, 23.viii.1925, Port Hacking, Sydney (A. Musgrave).

It is noteworthy that the majority of the species of the *T. rosea* group are absent from the Canberra area, although they have been recorded from Bateman's Bay. It would seem that temperature is not a major factor in restricting their distribution in New South Wales because they are well represented in the Blue Mountains area.

Recently a single specimen of *T. laetilinea* Walk. was collected at Blundell's, near Canberra, by Mr. I. F. B. Common and the author has also noticed it on blossom, but was unable to collect another species similar to *T. albimacula* Walk. at the same place. This provides evidence that the group is represented by odd species in the Canberra area, but apparently these occur rarely and fly comparatively late in the season (October).

2. Trichophthalma bivittata Westwood ♂, ♀ (= *eques* Schin. 1868)

Westwood, 1835, Phil. Mag. **6**: 448.

Bequaert stated (below the description of *T. bivittata wheeleri*) that *T. eques* Schin. is a synonym of this species.

The author can add the following localities: 2 ♂♂, 2.ix.1935, Gordon, N.S.W. (D. F. Waterhouse); 1 ♂, 13.ix.1925, Galston, N.S.W. (Wood); 4 ♂♂,

15.ix.1934, Narrabeen, N.S.W. (D. F. Waterhouse); 1 ♂, 28.viii.1934, Myall Lakes (Mungo), N.S.W. (D. F. Waterhouse); 2 ♂♂, 29.ix.1934, Blackheath, N.S.W. (D. F. Waterhouse); 2 ♂♂, 22.ix.1934, Killara, N.S.W. (D. F. Waterhouse); 1 ♂, 25.x.1930, Mt. Victoria, N.S.W. (A. Burns).

Among the typical specimens there is a new form not previously described, which differs by its distinctly bluish appearance. For this form the author proposes the name: forma *coerulea* nov. Specimens of this form have been examined from the following localities: 1 ♂, 1 ♀, 23.viii.1925, Gundamain, Port Hacking, near Sydney (A. Musgrave); the male type of this form is in the Australian Museum, Sydney, the female in the Division of Entomology Museum, C.S.I.R.O., Canberra; 1 ♀, 1.viii.1926, National Park, N.S.W. (Mackerras).

Trichophthalma bivittata wheeleri Bequaert

Bequaert, 1932, Pan-Pacif. Ent. 4: 163-6.

The following is Bequaert's description:

"Holotype and paratype female, and allotype and paratype male from Mullewa (28° 29′S. 115° 26′E.), in the sandplain region of south-western Australia, 14 and 18.ix.1931, at flowers (possibly of *Leptospermum*) (W. M. Wheeler). According to Dr. Wheeler, Mr. L. J. Newman of Perth collected additional specimens in the same locality.

A large, thick-set fly, superficially resembling *T. bivittata* Westwood, being greyish white, with a broad black median stripe over thorax and abdomen, partial black lateral stripes on the thorax, and broad black side margins on the abdomen; white stripes of abdomen more regular than in typical *bivittata* and with more woolly, somewhat matted white hairs; under side of body white.

Female: Integument of body black. Antennae, palpi, labrum of proboscis, and legs clove brown; hind tibiae and tarsi slightly infuscate; pulvilli bright reddish yellow, with black tips.

Body moderately pilose above, very densely covered with longer hairs on the ventral side. Vertex with erect black hairs as far down as the anterior ocellus; remainder of head (including the beard) with white pile, with an admixture of black or grey hairs, especially on the upper ½ of the frons and on the middle of the face. Eyes densely covered with almost russet pile, except in the lower ¼ where the hairs are sparser and white. Dorsum of thorax with moderately long and rather sparse, erect, greyish pile, mixed with black; the hairs along the side of the dorsum and on the hind margin of the scutellum considerably longer and denser, greyish white, mixed with black ones apicad of the wings; pleura and pectus densely covered with long, greyish white pile. Abdomen with erect, black hairs on the black areas; the 2 broad white bands, however, covered with much longer, greyish white hairs, which are woolly and somewhat matted down; venter with long, white, appressed hairs. Femora with long, white pile; tibiae and tarsi with very short, sparse, somewhat russet hairs. The integument is entirely covered with dull pruinosity, which is almost everywhere ashy grey, except on the conspicuous longitudinal black bands of

the dorsum of thorax and abdomen. On the thorax a nearly uniform, moderately wide, black band runs over the middle of the dorsum from the anterior margin to the hind margin of the scutellum; in its anterior ½ it is flanked on each side by a slightly narrower, curved, black stripe, which begins at the shoulder, is broadly interrupted before the transverse suture, and stops before the base of the wing; there is also an indication of a dull black area in the extreme hind corner, close to the sides of the scutellum. On the abdomen the median black stripe continues that of the thorax, but is nearly twice as wide, narrower posteriorly; on most segments it is fairly parallel-sided, but on the 3rd tergite it is much narrower at the anterior margin; the lateral black stripe on each side follows closely the side margin, being about as wide as the median stripe, and its line of demarcation from the white submedian stripe is fairly straight; the median and the 2 lateral black stripes unite along the hind margin of the 5th tergite, the following tergites as well as the ovipositor being dull black.

Head large, slightly flattened, as broad as the thorax, semi-elliptical in profile; kidney-shaped seen in front, the height about $\frac{4}{5}$ of the width. Frons flat, moderately wide; inner orbits converging upward from the insertion of the antennae (where the frons measures slightly over ½ the width of the eye at that level) to half way up the frons; its upper part and the vertex with subparallel sides and slightly less than ½ as wide as at the antennae; sides of face strongly divergent downward. Ocellar protuberance elongate and low, scarcely set off, with a faint median depression; ocelli placed in an isosceles triangle, the posterior ocelli less than ½ as far apart as from the anterior ocellus. Antennae moderately long, placed on the sides of the face, close to the lower orbits; basal segment slightly broader than long, truncate at apex; 2nd very short and wide; 3rd flattened, awl-shaped, with a deep but narrow constriction close to the base, apparently setting off a narrow ring or collar-like supernumerary segment; its basal $\frac{1}{3}$ with subparallel sides, then rather rapidly narrowed to a blunt point which continues into the 3-jointed style; style slightly shorter than the antennae, the basal 2 divisions long, though together shorter than the 3rd, the 1st division shorter than the 2nd. Face moderately swollen, its sides separated from the inner orbits by deep but narrow grooves; its upper median portion forming a wedge in the frons above the antennal pits. Proboscis of medium length, directed downward; measured along the labrum it is slightly less than the height of the head; labella large and thick. Palpi short, of normal thickness, protruding but little from the pilosity of the face; the 2nd segment small, not swollen and without noticeable apical pit. Body very broad and thickset, somewhat flattened dorsoventrally. Thorax distinctly broader than thick; the dorsum about as wide as long; the transverse suture marked on the sides only over about ¼ of the width of the dorsum. Scutellum large, semi-elliptical, cushion-shaped; the swollen hind margin slightly set off by a depressed line. Abdomen broad and flat. Valves of ovipositor flattened and leaf-like; the lower edge strongly convex. Legs moderately long and stout; hind tibiae and tarsi slightly thicker than those of fore and mid legs.

Wings slightly shorter than the body, over 3 times as long as wide, practically hyaline throughout; the veins dark clove brown. Venation of the typical

Trichophthalma type, showing only minor differences from that of *T. bivittata* or *T. rosea*; these differences being due only to individual variation and therefore not of specific value. As in the 2 species mentioned, the apical portion of the upper branch of the 5th longitudinal vein (M_{3+4}) is not in line with the remainder of the diagonal vein, but placed considerably more basad.

Length, not including ovipositor (to apex of tergites 5) 16.5 mm.; greatest width of abdomen 7-7.5; length of labrum of proboscis 4; length of wing 16; width of wing 4-4.3 mm.

Male: In most respects similar to the female. Eyes with longer pile, holoptic in the upper ½ of the frons; inner orbits touching each other over about ½ the distance between the anterior ocellus and the antennal pits (over more than twice the length of the upper, free part of the vertex).

Total length 16.5 mm.; greatest width of abdomen 5.5; length of labrum of proboscis 4; length of wing 15; width of wing 4 mm.

This insect is evidently the western race of *T. bivittata* Westwood (= *T. eques* Schiner) of Queensland and New South Wales. I have compared it with 2 females of typical *bivittata* from Herberton, Queensland, and with 1 male of that form from National Park, N.S.W. In both sexes of typical *bivittata* the 2 white longitudinal bands of the abdomen have irregular, jagged outer margins and are covered with sparser, erect, greyish white pile; in the female the upper part of the frons and the vertex are distinctly narrower than in the subsp. *wheeleri* (about ⅓ of the width of the frons at the insertion of the antennae); while in the male the inner orbits touch each other over a shorter distance (about equal to the length of the upper, free portion of the vertex).

Mr. F. W. Edwards, who very kindly examined for me Westwood's type at the British Museum, writes me that it is a female agreeing exactly in regard to the form of the abdominal white stripes and the abdominal hairs with specimens from eastern Australia received from Mackerras as *T. eques* Schiner. No definite locality was mentioned in the original description of *T. bivittata,* but since the type was given to Westwood by Shuckard, it came evidently from New South Wales, whence Shuckard about that time described several Hymenoptera."

The author has seen specimens from the following localities: 2 ♂♂, 1 ♀, Sept. 1940, Hattah, Vic. (F. E. Wilson; 1 ♂, Sept., Yelbeni, W.A. (B. A. O'Connor); 1 ♀, Pinjarra, W.A. (E. Goerling); 1 ♀, Sept. 1938, S.W. district, W.A. (E. H. Kipps); 1 ♂, Sept. 1938, Sand plains, Dumbleyung, W.A. (E. H. Kipps) (in this specimen the 3rd antennal joint is very dark); 1 ♂, 16.xii.1914, Geraldton (the date would appear doubtful for the remaining specimens are collected much earlier in the season).

3. Trichophthalma alulata, sp. nov. ♂, ♀

Very closely related to *T. bivittata wheeleri* Beq., but differs by the characters mentioned in the key; moreover, the black median and 2 longitudinal lateral stripes on the tergites are narrower than in *T. bivittata wheeleri* Beq. The author has examined only a single male and single female and cannot regard the other differences as constant. It is to be hoped that Western Australian

entomologists will collect series of these 2 forms so that a critical comparison can be made.

1 ♂, 16.viii.1940, Mingenew, W.A. (Mules), the type in the Western Australian Department of Agriculture; 1 ♀, "29—1504," Yerbillou, W.A. (Western Australian Museum).

4. Trichophthalma laetilinea Walker ♂, ♀

Walker, 1857, Trans. Ent. Soc. Lond. 4: 134.

The author has seen the material studied by Dr. Mackerras and can add the following localities: 1 ♂, 1 ♀, 5.xi.1924; 3 ♂♂, 9.x.1925; 1 ♂, 11.ix.1923; 1 ♀, 27.x.1927; 1 ♀, 6.xi.1927; 1 ♀, 28.x.1927, all from Stanthorpe, Queensland; 1 ♀, 22.ix.1942, Pittsworth, Queensland; 1 ♀, 4.x.1926, Medlow, N.S.W.; 1 ♀, 20.x.1930, Blackheath, N.S.W. (A. N. Burns); 1 ♂, 24.x.1950, Blundell's, A.C.T. (I. F. B. Common).

5. Trichophthalma ricardoae Lichtwardt ♂, ♀

Lichtwardt, 1910, Dtsch. ent. Z., p. 385.

The author can add only the following localities: 1 ♀, Kuranda, Queensland (F. P. Dodd); 1 ♀, 12.ix.1933, Hawkesbury Lookout, Blue Mountains, N.S.W. (G. A. Waterhouse); 1 ♀, 1 ♂, Oct. 1930, Mt. Victoria, N.S.W. (F. E. Wilson).

6. Trichophthalma albimacula Walker ♂, ♀

Walker, 1849, List. Dipt. Ins. Brit. Mus., vol. 2, p. 234.

The author can add the following localities: 1 ♀, 6.viii.1934, Killara, N.S.W. (D. F. Waterhouse); 1 ♂, 14.viii.1927, Cabbage Ck., Manly, Sydney; 1 ♂, 2.ix.1933, Collaroy, Sydney (G. A. Waterhouse); 1 ♂, 20.viii.1935, Stanthorpe, Queensland (H. Jarvis).

A male collected in September at Yelbeni, W.A. (B. A. O'Connor) from the Western Australian Department of Agriculture, differs from the typical eastern Australian form by the presence of reddish yellow spots of ground colour laterally at anterior corners of 2nd, 3rd, and 4th tergites. The hairs in these areas are long and whitish and contrast sharply with the deep black hairs on the remainder of the sides. The author proposes the name *T. albimacula occidentalis*, subsp. nov. for this form. It is probably closely related to *T. variolosa* Lichtw., but the latter species has not been studied sufficiently to enable the question of its systematic position to be decided.

7. Trichophthalma waterhousei, sp. nov. ♂, ♀

Very closely related to *T. albimacula*, and until the present time was confused with this species. Easily distinguished by the characters mentioned in the key. Moreover, the form of the alula is different in both sexes: in *T. albimacula* its basal part is triangular and the hind margin is straight; in *T. waterhousei* the alula is also triangular, but distinctly more acute and the basal part of its hind margin is distinctly concave. Hind tarsi and tibiae are darker than in *T. albimacula*.

It is very probable that this species belongs to 1 of the 2 forms distinguished by characters of the genitalia, mentioned by Mackerras, p. 539. The shortage of material makes it impossible to state this definitely. 2 ♂♂, 29.ix.1939, Blackheath, Blue Mountains, N.S.W. (D. F. Waterhouse); 1 ♂, 4.x.1926, Medlow, N.S.W.; 1 ♂, 25.viii.1923, Balli, N.S.W.; 1 ♀, Sydney (Ballard).

The type, male, in Division of Entomology Museum, C.S.I.R.O., Canberra.

8. Trichophthalma thomsoni, sp. nov. ♂

The author has examined the type of *T. bivittata* Thoms. 1868 (1 ♂, Sydney, Kinberg), a species which Mackerras regarded as a synonym of *T. albimacula* Walk. The type of *T. bivittata* Thoms. does not belong to *T. albimacula,* but to a new species. The name *bivittata* is preoccupied by Westwood, 1835. The author therefore names this species *T. thomsoni,* sp. nov.

It differs from *T. albimacula* Walk. by:

(1) Venation: the veins running from the apex of upper basal cell and discal cell are long, not point-like;

(2) Form of alula: it is very acute and concave at base, not straight;

(3) Black tarsi;

(4) Smaller size;

(5) Nearly equal size of facets at connecting line and at hind border of the eye (in *T. albimacula* they are much larger at connecting line).

Unfortunately the type specimen, which is otherwise well preserved, is without genitalia. Length of wing 9 mm. The type has been returned to the Stockholm Museum.

9. Trichophthalma variolosa Lichtwardt

Lichtwardt, 1910, Dtsch. ent. Z., p. 386.

The author has not seen this species.

10. Trichophthalma grisea Mackerras ♀, ♂ (new)

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 542.

The author has seen specimens from the following localities: 4 ♂♂, 3 ♀♀, 6.ix.1926, Kojarena, W.A. (E. W. Ferguson); 1 ♂, 1 ♀, Sept., Yelbeni, W.A. (B. A. O'Connor) (National Museum, Melbourne). (Both these specimens have the apical part of diagonal vein present and this continues in the same straight line of diagonal vein); 3 ♂♂, 2 ♀♀, Sept., Yelbeni, W.A. (O'Connor). (One female has in its right wing a complete diagonal vein as in the male and female mentioned above); 1 ♂, Mullewa, W.A. (L. J. Newman); 1 ♂, Sept., Yelbeni (on the left wing the diagonal vein is complete and forms a straight line); 1 ♀, 14.ix.1936, Hovea, W.A. (K. R. Norris); 10 ♀♀, 6.ix.1926, Kojarena, W.A. (A. J. Nicholson).

It is evident that as a rule the diagonal vein is without the apical veinlet, rarely it is present in only 1 wing and more rarely still the diagonal vein is complete in both wings.

The hind margin of scutellum as a rule is grey, not dark, but the type and 2 females from Yelbeni have the hind margin of scutellum black. There is also a slight difference in the markings of the mesonotum, which the author regards as only individual variation.

Male (*new*).—Very similar to the male of *T. primitiva,* but smaller. Head viewed from the front is distinctly broader than high (in *T. primitiva* the head is nearly as broad as high). Alula at base triangular (in female also) very acute. The transverse bands of hairs on abdomen (the longer whitish in anterior part and the shorter blackish in posterior part) are not so pronounced as in *T. primitiva.*

The female of this species can be readily distinguished from the female of *T. primitiva* by the presence of a median row of black spots and the very short hairs on the abdomen; the transverse bands of long hairs are absent. In general appearance the female of this species clearly differs from the male, whilst in *T. primitiva* there is a marked similarity between the sexes.

11. Trichophthalma primitiva Walker ♂, ♀

Walker, 1857, Trans. Ent. Soc. Lond. **4**: 134.

The author cannot add any new localities.

12. Trichophthalma scapularis Bigot ♂, ♀ (= *nigripes* auct.)

Bigot, 1881, Ann. Soc. Ent. Fr. (6) **1**: 20.

The author has seen the specimens studied by Mackerras and also specimens from the following localities: 1 ♂, 3.i.1948, Canberra, A.C.T. (S. J. Paramonov); 1 ♀, Mar. 1932, Bulli Pass, N.S.W. (D. F. Waterhouse); 1 ♂, 1 ♀, Jan. 1930, Stanthorpe, Queensland (H. Jarvis); 1 ♂, 6.xii.1927, Stanthorpe (E. Sutton); 2 ♂, 12, 30.xii.1924, Gravesend; 1 ♀, 2.xi.1935, Beerwah, Queensland (H. E. Young); 1 ♂, 2.ii.1930, Stanthorpe (W. B. Barnard); 1 ♀, Victoria; 1 ♀, 5.xii.1913, Stradbroke I., Queensland (H. Hacker) (a specimen with yellow legs, but with the abdomen not distinctly purplish); 1 ♀, Nov. 1918, Bribie I. (H. Hacker) (similar to the preceding specimen); 2 ♂♂, Jan. 1934, Eukey, S. Queensland (F. E. Wilson).

Authors have used the name *nigripes* Macq. for this species, but for several reasons the author thinks this name must be rejected:

(1) A detail of Macquart's description is inconsistent with this species: "thoracis lateribus, abdominisque incisuris flavipilosis." There are never yellow hairs at the margins of the abdominal segments of this species, the whole surface of the tergites being black-haired.

(2) Macquart gave no locality for this species, and there is no reason why it should be regarded as Australian.

(3) Head of the specimen described by Macquart was not from a member of this genus. Macquart himself noticed this when he wrote: "la tête . . . appatrient peut être à une Nemestrine ou à la Pangonie." His statement that the eyes are bare show us clearly that the description

of *T. nigripes* is certainly of an "artefactum," but not of any existing insect.

Dr. E. Séguy of the Paris Museum, where the type of *T. nigripes* is preserved, confirmed the artificial nature of the type.

(4) Although according to the international rules of nomenclature the description of one part of the body fulfils the requirements for naming, it is not clear what part of this insect was regarded by Macquart as authentic. In view of these facts, the author proposes to use the name *T. scapularis*, because Bigot was the first author who has given a recognizable description of the species.

TRICHOPHTHALMA SCAPULARIS var. PALLIPES, var. nov. ♂, ♀

This form has already been mentioned by Mackerras, but not named. Occasionally specimens with characters intermediate between this and the typical form have been collected, but geographical distribution shows that this form lives mostly in plains, in coastal areas, and has not been recorded south of Sydney. An examination of a large series of specimens of both sexes would be necessary to decide definitely the exact taxonomic rank of this form.

It differs by the clearly visible purplish tinge of abdomen, the undusted anterior part of the 2nd, 3rd, and 4th tergites, which are therefore darker than the remainder of abdomen, and by the yellow legs. Usually the hind tibiae and tarsi are dark, but there are also specimens with wholly yellow legs.

The author has seen specimens from the following localities: 1 ♂, Lake Macquarie, N.S.W.; 1 ♀, 21.i.1926, Tooloom, N.S.W.; 1 ♀, 5.xii.1913, Stradbroke I., Queensland (H. Hacker); 1 ♀, Kendall, N.S.W.; 1 ♀, Blue Mts., N.S.W.; 1 ♀, 1.iii.1917, Mt. Tambourine, Queensland; 1 ♂, 1923, MacPherson R. (H.T.); 1 ♀, 29.xii.1926, Biloela, Queensland (G. A. Currie). The type of new variety in Division of Entomology Museum, C.S.I.R.O., Canberra.

13. TRICHOPHTHALMA NIGROVITTATA Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 531.

The author has seen the material studied by Mackerras, and can add only one locality record: 1 ♂, 1.i.1921, Eccleston, N.S.W. (J. Hopson).

14. TRICHOPHTHALMA BANCROFTI Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 533.

The author has seen the material studied by Mackerras and also specimens from the following localities: 1 ♂, 2.xii.1913, Brisbane (H. Hacker); 1 ♂, 1925, Hughenden (H. H. Bachelor); 1 ♀, 24.ii.1943, Pomona (A. E. Horne); 1 ♂, Jan. 1929, Magnetic I., Queensland (J. W. Fieldny); 1 ♂, 12.iii.1926, Stanthorpe, Queensland; 1 ♂, Apr. 1928, Gogango, Queensland (F. Roberts); 2 ♂♂, 1 ♀, 3.i.1927, Goodna, Queensland (F. Roberts); 1 ♂, 1.i.1927, Brisbane (J. Mann); 1 ♀, 29.xii.1930, Toowoomba, Queensland (W. B. Barnard); 1 ♂, 3.xii.1922, Goodna, Queensland (A. Burns); 1 ♀, 6.i.1930, Mackay, north Queensland (A. Burns); 1 ♀, 24.i.1926, Tooloom, N.S.W. (H. Hacker).

15. Trichophthalma froggatti, sp. nov. ♂

Very similar to *T. bancrofti*, but differs by the characters mentioned in the key, which link it also with *T. novaehollandiae*.

1 ♂, 1919, Cairns, north Queensland (Jarvis), type; 2 ♂♂, Coen, north Queensland (W. D. Dodd); the type male in Division of Entomology Museum, C.S.I.R.O., Canberra; female unknown.

16. Trichophthalma doddi, sp. nov. ♂, ♀

Very similar to *T. novaehollandiae*, but differs in the characters mentioned in the key; perhaps a subspecies of *T. novaehollandiae*. The wings are extremely long, to 27 mm., but there are specimens smaller and with a respectively smaller length of wing.

1 ♂, Nov. 1926, Meringa, Queensland (Goldfinch), type; 2 ♀♀, Cairns District (Dodd); 1 ♀, Rockhampton, Queensland; 1 ♂, Pt. Curtis, Queensland. Type in Division of Entomology Museum, C.S.I.R.O., Canberra.

17. Trichophthalma novaehollandiae Macquart ♂, ♀

Macquart, 1840, Dipt. Exot., vol. 2, p. 19.

The author has seen the material studied by Mackerras, and can add the following locality records: 3 ♂♂, 1 ♀, 2.xi.1927, Stanthorpe, Queensland (S. M. Watson); 1 ♀, 4.xii.1935, 1 ♂, Oct. 1937, Brisbane (A.R.B.); 1 ♂, Nov. 1914, Urala, N.S.W. (W. W. Froggatt); 1 ♂, 6.x.1914, Brisbane (H. Hacker); 1 ♂, 3 ♀♀, 21.i.1948, Tubrabucca, Barrington Tops, N.S.W. (A. Burns).

It is noteworthy that one female from Gordonvale, Queensland (10.i.1922, W. C. Dormer) belongs to this species and not to *T. doddi*, sp. nov.

18. Trichophthalma fullerae, sp. nov. (= partim *T. obscura* Westw. *sensu* Macker.)

The author thinks it is necessary to change the name of this species and to use other characters for distinguishing it from the remaining forms.

Mackerras has used Westwood's name for this species, but regards *T. obscura* as "somewhat doubtful." Westwood's description (Mackerras, p. 515) is only 3 lines in length and he states: "Habitat in Africa?" Hardy (1924) was the first author to apply the name *obscura* to an Australian species of this group. However, the species of Hardy and Mackerras is without doubt not *T. obscura* Westw. In the original description, "ocello antico aliis remotis," whereas in the species of Mackerras the anterior ocellus is in the usual position. Moreover, Mackerras described under the name *obscura* 2 forms (slender and stout), which may represent 2 different species.

The author proposes to delete *T. obscura* Westw. from the list of Australian Nemestrinidae, because the locality of the type is doubtful (perhaps Africa) and the position of the anterior ocellus in Australian species is different.

This species belongs to the *T. costalis* group, but is readily distinguished by the following characters: either mesonotum or abdomen have well-marked whitish, grey, yellow, or black striping; the distance between the anterior ocellus

and the hind margin of the ocellar tubercle is a little greater than that between the outer sides of the lateral ocelli.

Alula broad, at base only subacute, rounded; viewed from above the last tergite is similar to Figure 6*a* or 6*h* of Mackerras, i.e. with a poorly developed median tubercle; frontal keel is present on the upper part, undivided, the furrow between the sides of the face and the inner margins of the eyes being practically absent; frons with 2 tufts of white hairs at the sides above base of antennae.

The whole body is covered with greyish brown dust, which in some parts is more grey while in others it is more brown.

There is a median row of small darker spots on tergites; the sides of tergites are also a little darker, spot-like; the anterior border of the 2nd, 3rd, and 4th tergites may have a narrow, darker, transverse, somewhat obscure band. Under side of body whitish. Halteres yellow or dirty yellow.

The eyes connect at 1 point rather remote from the anterior ocellus (there is a very narrow separating triangle nearly as long as the ocellar triangle).

Length of body 12.5-14.5 mm., of wing 12-13.5 mm.

2 ♂♂, 31.xii.1933, Crookhaven, N.S.W. (M. Fuller); 1 ♂, 10.xii.1933, Cotter River, near Canberra (M. Fuller); 1 ♂, 1.i.1930, Stanthorpe, Queensland. The specimens from Crookhaven are very similar, the specimen from Cotter River is a little smaller and paler, the specimen from Queensland has a well-pronounced transverse band of white hairs at the base of abdomen, but the author regards this as only individual variation.

Type in Division of Entomology Museum, C.S.I.R.O., Canberra.

Note.—The author has seen several specimens of this species identified by Mackerras as *T. obscura* Westw.; the synonymy: *T. fullerae*, sp. nov. = *T. obscura* Westw. *sensu* Macker. is without doubt.

19. Trichophthalma mackerrasi, sp. nov. ♂

Superficially very similar to *T. fullerae*, sp. nov., but easily distinguished by the alula having a nearly straight hind margin and being distinctly acute-triangular at base; by the position of its anterior ocellus, which is twice as far from the posterior ocelli as they are from each other; by the completely bare frons; and by the genitalia.

This species conforms somewhat to the description of *T. obscura* Westwood, but the author prefers to use a new name instead of a very disputable interpretation of Westwood's species.

4 ♂♂, 18.x.1930, Stradbroke I., Queensland, near Brisbane (one of these specimens was identified by Mackerras as "? *T. subcostalis*, not quite typical," but *T. subcostalis* was described from South Australia, and it is very possible that it is only a subspecies of *T. rufonigra* (see the description of Mackerras).

Length of body 15-19.5 mm., of wing 14.5-18.5 mm. Type in Division of Entomology Museum, C.S.I.R.O., Canberra.

20. Trichophthalma fusca Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 516.

The author has examined the types (male and female) and can add:

Male.—Alula triangular. Whole surface of frons with very long hairs. Frontal keel very weak. Third joint of antennae dark, distinctly longer than 2 basal yellow joints together. Furrow between the face and cheeks narrow, but clearly visible. Ocellar triangle nearly equilateral.

Female.—Ocellar triangle and 3rd joint of antennae as in male. Frons also with long and dense white hairs, only a narrow median stripe is bare. Sides of face long-haired as in male.

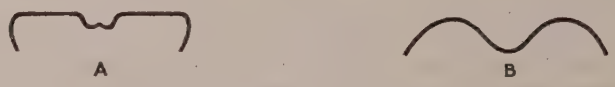

Fig. 5.—*A*, the last tergite of *Trichophthalma fusca* Macker. viewed from above; *B*, same of *T. calabyi*, sp. nov.

21. Trichophthalma calabyi, sp. nov. ♂

Differs from all *Trichophthalma* species (excluding only *T. fusca*) by the particular form of its last tergite.

Ground colour of body dark brown, only femora and tibiae mostly yellow-reddish. Ocellar triangle not very high, and only a little longer than its width. Eyes nearly joined. Eyes mainly black-haired, but with whitish hairs below. Frons nearly bare, with 2 rows of whitish hairs along the inner margins of the eyes. Antennae dark; the face is rather protruding. Palpi dark, black-haired. Proboscis long, nearly twice as long as the head.

Mesonotum uniformly grey-dusted, without well-marked stripes or spots, with short, erect, dark hairs intermixed with a small number of yellowish. Sides of mesonotum with very dense, longer, and stronger black hairs; some are nearly bristle-like. The under side of thorax is covered with very dense and long grey-whitish hairs. Scutellum similar to mesonotum but with black and whitish distinctly longer hairs on the hind margin.

Wings hyaline, greyish, with very well-marked, darkened areas on the anterior border, similar to that of *T. costalis*. Alula well developed, much narrower towards the base, but this region is not acute, but slightly rounded. Halteres dark; tarsi (except the anterior) black.

Abdomen dark, grey-dusted above and nearby, whitish below. Adbomen has very characteristic pattern; on the anterior margin of the 2nd, 3rd, and 4th tergites there is a narrow but clearly visible dark fascia; the lateral margin of the tergites has a dark longitudinal, regular, uninterrupted stripe. There is also a median, uninterrupted, narrow black stripe, consisting of elongated spots. The hind margin of the last tergite is emarginated; the size of the incision is nearly the same as the size of the lateral lobes. Genitalia typical: the lower middle plate is broad at base, triangular, shorter than the lateral forceps, nearly equilateral (in *T. fusca* the middle plate is higher and its apex is acute).

The hairs on the upper side of the abdomen are uniformly distributed, black; on the anterior border of the second tergite they are nearly white, but this is

visible only under the lens and does not give the impression of the white bands of *T. costalis*.

Length of body 14 mm., of wing 13 mm.

1 ♂, 20.x.1947, Immarna, S.A. (J. Calaby).

The type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

22. Trichophthalma intermedia Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 517.

The author has examined the types. A species very closely related to *T. rufonigra* but differs by its undivided frontal keel in both sexes and the distinctly longer ocellar triangle in both sexes (in the male of *T. rufonigra* the ocelli form a nearly equilateral triangle; in the female of *T. rufonigra* the ocelli are distinctly not equilateral, but the anterior ocelli are separated by a cross furrow from the posterior ones and placed not as high as in the female of *T. intermedia*). In both sexes the furrow between the sides of the face and the inner margins of the eyes is not so clearly pronounced (in *T. rufonigra* this furrow is nearly as broad as the last joint of palpi). Frons in both sexes quite bare (in *T. rufonigra* narrowly haired at the sides). Form of alula similar. The median longitudinal dark stripe of abdomen is very narrow, at most as broad as $\frac{1}{5}$ of the width of the abdomen.

Structure of the head as in *T. rufonigra*, but not as in *T. bancrofti*.

23. Trichophthalma costalis Westwood ♂, ♀

Westwood, 1835, Phil. Mag. **6**: 448.

The author has seen all the material studied by Mackerras and also specimens from the following localities:

1 ♂, 12.ix.1918, 1 ♂, 29.viii.1920, Bribie I., Queensland (H. Hacker); 1 ♂, 30.ix.1921, Brisbane (H. Hacker); 1 ♂, 28.xii.1911, Tambourine Mountain (H. Hacker); 1 ♂, 30.xi.1910, Sydney, 1 ♂, 11.xii.1912 (W. W. Froggatt); 1 ♂, 1.xii.1911, Loftus, N.S.W.; 1 ♂, 25.x.1912; 1 ♀, 6.xii.1912, Sydney (McCarthy); 1 ♂, Dec. 1911, Gilgai, N.S.W. (W. W. Froggatt).

Trichophthalma costalis soror, subsp. nov. ♂

This is a western subspecies of *T. costalis*. It is very similar to the typical subspecies, but differs by:

(1) Not so pure white band at base of abdomen;

(2) More greyish tergite integument;

(3) Distinctly different genitalia.

Viewed from the ventral side, the median genital plate (ninth sternite) is long and in the shape of high isosceles triangle; the space between the apical part of this plate and the lateral forceps is almost linear (in *T. costalis* the apical part of this plate is tapering and the space between the plate and the lateral forceps is nearly semicircular, because the inner margins of the forceps are distinctly excavated).

Upper part of face is usually dark.

4 ♂♂, 27.x.1940, City Beach, W.A. (P. N. Forte), type; 1 ♂, Rottnest I., near Perth; 2 ♂♂, 3.xi.1940, Floreat Park, W.A. (P. N. Forte).

The type in Division of Entomology Museum, C.S.I.R.O., Canberra.

24. Trichophthalma apicalis Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 512.

The author has seen specimens from following localities: 1 ♂, Swan River, W.A. (L. J. Newman); 1 ♂, 6.xi.1947, Byford, W.A. (A. Burns).

25. Trichophthalma rufonigra Mackerras ♂ ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 513.

One of the commonest species during the summer in areas higher than 3,000 ft. on *Leptospermum* and *Kunzea*.

To the localities and data mentioned by Mackerras the author can add: ♂♂, ♀♀, 4.ii, 9.ii, 13.ii, 19.ii.1948, Bendora, A.C.T. (S. J. Paramonov), 30.i.1948, 23.iv.1948, 13.iii.1948, 31.iii.1948, Blundell's, A.C.T. (S. J. Paramonov); 1 ♂, 3 ♀♀, Jan. 1939, Mt. Kosciusko, N.S.W. (D. C. Swan); 1 ♂, Dorrigo, N.S.W. (W. Heron).

26. Trichophthalma subcostalis Mackerras ♂

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 514.

The author has seen the type and has made the following notes:

Surface of wing distinctly yellowish. Alula well developed, as in *T. rufonigra*, but not so much as in *T. costalis*.

Ocellar triangle nearly equilateral (in *T. rufonigra* distinctly elongated). Frons line at narrowest point sunken (as in *T. costalis*). Furrow between the face and eyes very narrow, poorly visible. Face in profile very protruding.

Thorax uniformly yellowish-dusted, without 2 whitish small spots, which occur usually in *T. rufonigra*. Abdomen red, dark median stripe is nearly parallel-sided, occupying less than $\frac{1}{3}$ of segment width.

27. Trichophthalma transversa, sp. nov. ♂

This species belongs to the *T. rufonigra* group.

Ground colour of body black, except sides of 2nd, 3rd, and 4th tergites, which are broadly yellow-reddish. Femora and tarsi of all legs black or blackish, tibiae reddish. Ocellar triangle not equilateral, a little elongated but in general short. Touching line of eyes is long, but not complete. Upper part of frons with short but distinct keel. Sides of frons broadly clothed with short, erect, yellowish hairs. Facets nearly equal, in general small. Whole frons grey-dusted. Antennae black; 1st and 2nd joints nearly equal, 3rd joint elongated, conical, with very long, 3-jointed style. Face a little shining, not dusted, very sparsely haired, in profile not so protruding as in *T. rufonigra*. Touching line is not depressed, sunken, as in *T. costalis*. Furrow between the face and eyes very narrow, nearly invisible. Hairs on facets yellowish. Viewed from front the

lower part of face is much higher than the lower line of the eyes (in *T. rufonigra* only slightly higher).

Mesonotum and scutellum dark, with short black and yellowish hairs; mesonotum without 2 small whitish spots at sutura. Under side of thorax dense whitish-haired. Halteres yellow. Wings hyaline but with well-marked brownish suffusion along anterior margin (¾ of the length). Alula broad, distinctly longer than broad, a little broader than axillary lobe, at base not triangular but rounded.

Under side of abdomen reddish, with very dense whitish hairs. Ground colour of tergites yellow-reddish, with a narrow, black, not regular median stripe, and darkened hind margins on 2nd, 3rd, and 4th tergites; these transverse dark bands are not very deep black, but are clothed by black hairs and therefore seem darker. At sides these bands are a little broader. Longitudinal dark lateral stripes completely absent in this species.

The median genital plate (ninth tergite) is triangular, broad, comparatively broader than in *T. rufonigra*. The dark median stripe of tergites is at most ⅓ width of tergite (in *T. rufonigra* nearly ½).

Length of body 17 mm., of wing 15.5 mm.

1 ♂, Eidsvold, Queensland (Bancroft). Type in Division of Entomology Museum, C.S.I.R.O., Canberra.

28. Trichophthalma punctata Macquart ♂, ♀

Macquart, 1846, Dipt. Exot. Suppl. 1: 101.

This species was described from Tasmania. The author has examined a lengthy series of specimens, and can state that there are at least 3 forms of this species in Tasmania. It is very possible that *T. quadricolor* Walk. and other species which are regarded now as synonyms in fact represent forms of different taxonomic value.

The author prefers to denote these in a preliminary way as *"a," "b," "c."*

Forma *"a"*.—This form differs clearly by the presence of black hairs at the sides of the 2nd and 3rd tergites, which form black tufts; by the larger black spots on the median stripe; by the blackish anterior border of the 3rd and 4th tergites (these tergites seem to have narrow black fasciae); and by the brighter orange-yellow ground colour of the abdomen. This form the author has seen only from Tasmania and is apparently absent from the Australian continent.

Forma *"b"*.—The author regards this as the typical form. The black hairs on the sides of 2nd and 3rd tergites are very sparse or absent; the black spots on the median line of the abdomen are narrow, elongated; the anterior border of the 3rd and 4th tergites is grey-dusted; the yellowish ground colour of abdomen is paler, and often the predominating colour is grey rather than yellow.

In general appearance form "b" is more greyish and has been taken more commonly than *"a"* (in ratio 2:1). There are also all intermediate forms, but form *"a"* is limited geographically.

Forma *"c"*.—Much smaller and greyish and distinguished readily from the preceding forms by the triangular alula which is distinctly acute at base. This form the author has seen also from the mainland, but there are comparatively few specimens.

All the characters mentioned refer only to the males; the differences in the females are not yet known.

1 ♂, 22.xii.1927, Stanthorpe, Queensland (E. Sutton); ♂ ♂, St. Mary's, Tas., also Hobart, Launceston, St. Helens, Tas.; 1 ♂, "South Austr."; 1 ♂, 29.xi.1930, Bunya Mts., Queensland (E. Sutton); 1 ♂, 10.ii.1929, Ferntree Gully, Vic. (A. Burns); 2 ♂ ♂, 2.i.1946, Heathmont, Vic. (A. Burns); 2 ♂ ♂, 10.ii.1929, Millgrove, Vic. (F. E. Wilson); 2 ♂ ♂, 17.xii.1929, Ringwood, Vic. (F. E. Wilson).

29. Trichophthalma orientalis Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 519.

This form was described by Mackerras as *T. punctata orientalis* Macker., but the marked difference in the genitalia shows that it is a closely related, but doubtless a separate species. Therefore the species could have the name *T. orientalis* Macker.

The author has seen specimens from the following localities: 1 ♂, Feb. 1932, Boonya, W.A. (Miss A. E. Baesjo) (National Museum, Melbourne); 1 ♂, 11.ii.1928, Belgrave, Vic.; 2 ♂ ♂, Toronto, N.S.W. (Filmer); 1 ♂, 20.iv.1925, Stanthorpe, Queensland; 1 ♂, 15.ii.1933, Gisborne, Vic.

30. Trichophthalma fulva Walker

Walker, 1849, List. Dipt. Ins. Brit. Mus., vol. 2, p. 235.

The author has seen 3 specimens (males) in Australian Museum, which were identified by Mackerras as *T. fulva* Walk. In the specimen from King George Sound examined by Mackerras, the frontal keel is replaced by a furrow. Alula long, narrow, triangular. Both Queensland specimens have a keeled frons and one also has a distinctly more rounded alula.

It is noteworthy that the striping of the mesonotum in *T. fulva* is not always very well marked; often it is indistinct (it apparently depends upon the condition of the specimen). The genitalia of the Queensland specimens differ from that of the Western Australian specimen; the latter has the 9th sternite narrow, elongated, and closely adjacent to the lateral forceps. It would seem therefore that the Queensland specimens represent a separate species.

31. Trichophthalma lutea, sp. nov. ♂

Closely related to the Western Australian *T. fulva* Walk.

Eyes covered with long and dense dark hairs, except on the lower portion where they are replaced by the yellowish ones. The line separating the eyes is very narrow, much narrower than the anterior ocellus. Ocellar triangle a little elongated, nearly equilateral. Ground colour of frons and face dark, yellowish pollinose. Keel in the upper ½ of frons absent (there is a very shallow longitudinal furrow). Frons densely yellowish-haired, but at antennal sutura bare. Antennae dark brown, nearly black, the 1st joint yellow-dusted. Third antennal joint long conical, distinctly longer than 2 basal joints together, and the 2 basal joints of arista. Basal joints black-haired. Long and numerous black hairs cover

the sides of face. Palpi black, with long black hairs. Between the eyes and face there are well-marked furrows. Proboscis twice as long as the head. Under side of head with long and extremely dense yellowish and whitish hairs.

Mesonotum dark, nearly black, with 2 broad lateral longitudinal yellowish stripes and 2 narrow submedian stripes; the submedian stripes are nearly as broad as ocellar triangle and a little coverging towards the scutellum, which is dark. Mesonotum and scutellum are covered with bright yellow hairs intermixed with fine black hairs on the sides of mesonotum. The depressed yellowish hairs concentrated mostly in front of scutellum, the remainder of mesonotum only with erect hairs. Legs and halteres yellow.

Wings nearly hyaline, with an almost invisible yellowish nuance. Alula very well developed, but at base acute, having triangular form.

Under side of abdomen and thorax nearly pure white-dusted and haired. The ground colour of abdomen is bright yellow-orange, with similar long and dense hairs, but there are also the fine, black, intermixed hairs.

On the median $\frac{1}{7}$ of abdomen there is a complete dark longitudinal stripe, which is nearly regular and darker than in *T. punctata*, without the darker spots (it is almost the same colour as the dark spots on the median stripe in *T. punctata*).

Genitalia well developed; the lower genital plate is large, at its base much larger than the lateral plates. The latter are a little longer than the lower plate and cover its apex in form of an arc. Genitalia of the type of *T. orientalis* Macker.

Length of body 12 mm., of wing 12 mm.

1 ♂, 31.xii.1933, Crookhaven, N.S.W. (M. Fuller), type; 1 ♂, 31.xii.1935, Mallacoota, Vic. (M. Fuller).

Type in Division of Entomology Museum, C.S.I.R.O., Canberra.

32. Trichophthalma leucophaea Walker ♂, ♀

Walker, 1849, List. Dipt. Ins. Brit. Mus., vol. 2, p. 233.

The author has seen specimens from the following localities: 4 ♂♂, Nov., Swan River (L. J. Newman); 1 ♂, Oct., Gnangara (B. A. O'Connor); 1 ♀, Nov., Swan River (B. A. O'Connor); 3 ♂♂, 10.xi.1934, Crawley, W.A. (K. R. Norris); 5 ♂♂, 3 ♀♀, 17.xi.1933, Perth, W.A. (M. Fuller); 1 ♂, 2 ♀♀, 4.xi.1936, Perth, Kings Park (K. R. Norris); 1 ♂, 1 ♀, 23.x.1946, Yanchep, W.A. (K. R. Norris); 1 ♀, 21.x.1932, Koorda, W.A. (Perry).

The very sharply marked striping of mesonotum and abdomen is a very easily recognizable character of this species. A broad median, uninterrupted, regular brown stripe, which is twice as broad as 2 greyish submedian stripes, is also a very good character for separating it from all closely related species.

33. Trichophthalma degener Walker, ♂, ♀

Walker, 1849, List. Dipt. Ins. Brit. Mus., vol. 2, p. 233.

"mas.—Fusca, subtus, alba, thorace fulvo univittate et albo bivittato, abdomine albo bivittato, lateribus flavo-fuscis, antennis fulvis piceo cinctis apice nigris, pedibus ferrugineis, alis subcinereis."

"Body rich brown, white beneath: head white, thickly clothed beneath with white hairs: eyes red, thickly clothed with white down; sucker black, as long as three-fourths of the body; palpi ferruginous; third joint piceous at the tip; feelers tawny; third joint piceous, short-conical; bristle black; chest like that of *H. leucophaea,* but having only a tuft of tawny hairs on each side; scutcheon dark ferruginous, with no white band; breast thickly clothed with white hairs: abdomen yellowish brown on each side, and having on the back two broad white stripes, which are more irregular than in the preceding species, and diverge along the fore borders of the segments to the sides of the abdomen: legs ferruginous: wings slightly gray; wing-ribs and fore border veins dark ferruginous; the other wings black; poisers tawny. Length of the body 6 lines; of the wings 12 lines" (Walker).

The author has seen specimens identified by Mackerras as *T. longirostris* Macker.; they, however, agree well with the description of *T. degener.*

Both *T. leucophaea* and *T. degener* are Western Australian species with a reddish yellow, grey-pollinose scutellum (the other members of this group have a dark scutellum). Both species are very similar, but nevertheless distinct.

The greyish submedian stripes of the mesonotum are broader than in *T. leucophaea* (nearly as broad as the dark median), but their boundaries are not so sharply marked.

The dark median stripe of tergites is comparatively narrow, narrower than the grey submedian stripes, and consists of isolated or semi-isolated brownish rounded spots; in *T. leucophaea* the brown and grey stripes are sharply contrasted whereas in *T. degener* the boundaries of these stripes are not sharply marked. Alula in both sexes as in *T. leucophaea* triangular, at base distinctly acute.

The author has seen specimens from the following localities: 1 ♂, Mar., Swan River, W.A. (L. J. Newman); 2 ♀♀, Feb., Swan River, W.A. (B. A. O'Connor); 4 ♂♂, Feb. 1930, Gnangara; W.A. (Perry); 2 ♀♀, 3.ii.1934, Lake Gnangara, W.A. (K. R. Norris); 1 ♂, Pinjarra, W.A. (L. J. Newman).

34. Trichophthalma regina, sp. nov. ♂

This species belongs to the *T. leucophaea* group, and is very closely related to *T. griseola,* sp. nov.

From *T. griseola* it differs by its very poorly developed longitudinal striping of mesonotum, by the long conical 3rd joint of antennae, and by the very short 2 basal joints of arista which are together distinctly shorter than the 3rd antennal joint.

From *T. leucophaea* it differs by the developed striping of the mesonotum, and by the comparatively narrow median stripe of the tergites; all 5 bands of abdomen are almost of equal breadth (in *T. leucophaea* the median dark stripe is distinctly twice as broad as the submedian greyish stripe), scutellum dark, etc.

At its narrowest point the frontal stripe is nearly as broad as the anterior ocellus. It is comparatively much narrower than in *T. leucophaea.* Ocellar triangle distinctly elongated, hairs on ocellar triangle dark, very long hairs on eyes—yellowish brown, beneath whitish. Hairs on frons, face, antennae, and

palpi yellowish, but at apex of palpi there are short black hairs, palpi yellow, but apex itself is black. Palpi distinctly 3-jointed, and may in fact have 4 joints. A furrow between the face and the eyes is very narrow, but distinctly visible. Basal joint of antennae yellow, the remainder dark.

Mesonotum greyish with 2 nearly imperceptible more brownish stripes. Hairs very fine, in disc blackish, at sides yellowish; under side with a very strong white dust and with white hairs.

Legs yellow, hind tibiae and tarsi with short black hairs. Halteres yellow. Wings greyish, along the anterior border darker, without a sharp boundary between subhyaline and darkened areas. Alula triangular, very acute at the base.

Abdomen with 3 well-developed brown stripes (median, and 2 lateral) and 2 well-developed greyish submedian stripes of nearly equal width; the brown stripes taper slightly toward the tips; the greyish are nearly parallel-sided.

Length of body 13 mm., of wing 12 mm.

2 ♂ ♂, Feb. 1932, Booanya, W.A. (Miss A. E. Baesjou). Type in Division of Entomology Museum, C.S.I.R.O., Canberra.

35. Trichophthalma griseola, sp. nov. ♂

Very similar to *T. regina,* sp. nov., but with well-developed striping of mesonotum.

Very similar to *T. regina,* but palpi are wholly yellowish; the black hairs are almost absent. Antennae black. Third joint of antennae short, conical, as long as 2 basal together, and as 2 basal joints of arista.

Mesonotum brown, with 2 very well-developed, narrow, greyish stripes, which are nearly parallel-sided and parallel one to another. Hairs on mesonotum, particularly on scutellum, yellowish (in *T. regina* the black hairs are dominant). There are no long dark hairs in form of fan on the mesonotum aside of scutellum, which are present in *T. regina.*

Wings nearly hyaline with very narrow, but well-developed and sharply separated dark stripe along the anterior border. Genitalia as in *T. regina*; the lower genital plate is long, narrow, narrower than the lateral plates.

Length of body 12.5 mm., of wing 11 mm.

1 ♂, 16.xi.1941, Katanning, W.A. (K. R. Norris). Type in Division of Entomology Museum, C.S.I.R.O., Canberra.

36. Trichophthalma confusa Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 521.

The author has seen specimens from the following localities:
1 ♂, 14.ii.1926; 1 ♂, 13.xii.1934, Killara (D. F. Waterhouse); 5 ♂ ♂, 1.i.1926, National Park, N.S.W. (I. M. Mackerras); 2 ♂ ♂, 30.xi.1925, Woodford, N.S.W. (I. M. Mackerras); 1 ♂, 7.xii.1931; 1 ♂, 30.x.1943, Como, N.S.W.; 1 ♂, 29.i.1933; 1 ♂, 5.i.1936, Wee Jasper, N.S.W., 3,000 ft. (M. Fuller); 3 ♂ ♂, 2 ♀ ♀, 28.i.1933, Mt. Kosciusko, N.S.W., 4,000 ft. (I. M. Mackerras); 1 ♂, 2.ii.1927, Mt. Kosciusko, N.S.W. (Harrison); 2 ♂ ♂, 31.xii.1933, Sassafras, N.S.W. (M. Fuller); 1 ♂, 3.i.1937, Countegany, N.S.W. (M. Fuller); 2 ♂ ♂, 23 and 31.ii.1948, Blundell's,

near Canberra (S. J. Paramonov); 2 ♂♂, 31.xii.1933, Crookhaven (M. Fuller); 1 ♂, 19.xi.; 2 ♂♂, 26.xi.; 1 ♂, 10.xii.1932, Berowra, N.S.W. (G. A. Waterhouse); 1 ♂, Dec. 1911, Gilgai, N.S.W. (W. W. Froggatt); 1 ♂, 9.xii.1921, Loftus, N.S.W.; 3 ♀♀, 25.i.1935, Yarrangobilly, N.S.W. (M. Fuller).

It is noteworthy to add that the male has a keel on upper ½ of frons. long palpi, protruding rather far beyond the apex of the face.

There are two forms of this species: one it seems occupying the coastal area, with rather bright yellow abdomen and comparatively few developed dark longitudinal stripes on abdomen; the second apparently occupying mountain areas, with greyish yellow submedian lateral spots and more developed blacker sides of the tergites.

37. Trichophthalma nicholsoni Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 525.

The author has seen the type and has made the following notes:

Male.—Alula triangular. Ocellar triangle distinctly not equilateral. Keel on frons absent, replaced by a small furrow. Mesonotum with 5 distinct whitish stripes (female also). Palpi yellow, hairs of frons and face yellowish.

On a genitalia preparation the author cannot discern 2 subacute submedian tubercles, and the median line is only slightly waved, nearly straight.

Female.—With very broad dark median stripe on abdomen and 2 sharply marked sublateral greyish stripes. Ocellar triangle elongated.

The author has seen specimens from following new localities: ♂♂, ♀♀, 9, 13, 19.ii.1948, Bendora, A.C.T. (S. J. Paramonov); ♂♂, ♀♀, 8.i.1938, Alpine Creek, Kiandra, N.S.W. (J. M. Mackerras); ♂♂, ♀♀, 26.i.1936, Alpine Creek, Kiandra, N.S.W. (T. G. Campbell); 1 ♂, 2 ♀♀, 19.i.1935, Blundell's, near Canberra, A.C.T. (M. Fuller); 3 ♂♂, 3 ♀♀, 28.i.1935, Yarrangobilly, N.S.W. (M. Fuller); 1 ♂, 2.ii.1927, Mt. Kosciusko, N.S.W. (Harrison); 3 ♂♂, ♀♀, 26.i.1935, Kiandra, N.S.W. (M. Fuller).

The female of this species is extremely similar to that of *T. bivitta*, but differs as a rule by its larger size, by the striped mesonotum, by the absence of golden hairs on mesonotum and on the greyish submedian stripes of abdomen, and by the broader median stripe of abdomen, which is distinctly broader than the greyish submedian stripes, whereas in *T. bivitta* these stripes are nearly equal.

38. Trichophthalma dubiosa Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 527.

The author has seen the type, and the following notes have been made:

Male.—Alula triangular. Frons with a keel. Face with dense, long, black hairs. Palpi extremely long. Femora dark. Striping of mesonotum is very well developed. Abdomen above with a narrow brown median stripe, lateral dark stripes poorly developed; sublateral yellowish grey stripes are broad, but not

sharply contrasting with brown ones. The 3 genital plates nearly equal in width, with long white hairs; the lateral plates a little longer than the median, and overhanging it.

Female.—The dark hairs on face are very long and dense. Femora yellow. Mesonotum very well striped. Lateral dark stripes on tergites not very well developed, the median dark stripe broader than that in male. The external angles of the 2nd, 3rd, and 4th joints of anterior tarsi with acute prolongations (tubercles). The face and frons in both sexes are dark yellowish brown. No additional material has been examined.

39. Trichophthalma bivitta nigricosta Mackerras

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 524.

The author has seen the type and has made the following notes: In male the striping of mesonotum is poorly developed, but visible; in female it is more distinct. Frons with keel. Palpi dark. Femora yellow, but darkened. Female.—Ocellar triangle elongated. Frons densely haired. Palpi darkened.

40. Trichophthalma trilinealis Mackerras ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 526.

The author has seen the type and has made the following notes: Face and frons whitish, a little shining. The hairs on ocellar triangle very long, black, dense. Below the ocellar triangle on frons there are 6 black, erect, hairlike bristles. The joints of anterior tarsi are acute at sides, but equal internally and externally. Palpi dark. Alula at broadest point is distinctly narrower than the axillary lobe (in the female type of *T. nicholsoni* it is nearly as broad). The dark median stripe of abdomen is not so sharply marked, and not so broad as in *T. nicholsoni*.

No additional material has been examined.

41. Trichophthalma ruficosta Mackerras ♂

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 522.

The author has seen the type and has made the following notes: Alula triangular, a little narrower than the axillary cell. Median genital plate very long, narrow, conical, much narrower than the lateral plates. Ocellar triangle not equilateral, a little elongated. Frons with a keel. Face in profile very protruding. Furrow between the face and eyes clearly visible. Frons haired. Prefurca of r_4 and r_5 much larger than that part of the "diagonal" vein directed towards the hind margin. The hind margin of the last tergite when viewed from above is nearly straight.

The lateral stripes of abdomen are well developed, as broad as the median stripes and both occupy about $\frac{1}{7}$ of the width of the segments. The median dark stripe is very regular, with parallel sides. The 3rd antennal joint is very elongated. The 3rd joint of antennae very elongated, conical. No further material has been examined.

42. Trichophthalma griseolineata Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 528.

The author has seen the type and has made the following notes: General appearance as in *T. ruficosta*, but smaller, and the median dark stripe of abdomen distinctly broader.

Male.—Alula triangular. The striping of mesonotum very distinct, but in female type it is not clearly visible, because the specimen is not in good state of preservation. Face in profile very protruding. The furrow between the face and eyes absent. Upper part of frons with a keel. Frons bare, with 2 tufts of whitish hairs above the base of antennae. Facets in the upper part of the eyes and at inner part of them are distinctly larger than in the lower part and the external areas. Viewed from the front the horizontal diameter of the head is slightly greater than the vertical. Ocellar triangle elongated, not equilateral. Frons and face narrow. The median broad, dark stripe of abdomen is not parallel-sided, but consists of trapezoid spots.

Female.—The antennal joint is as in male pear-like, not elongated, a little shorter than 2 basal joints together. Face densely dusted, not shining.

No further specimens have been examined.

43. Trichophthalma harrisoni Mackerras ♂, ♀

Mackerras, 1925, Proc. Linn. Soc. N.S.W. **50** (4): 525.

The author has seen specimens from the following localities:

Barrington Tops, N.S.W. (typical material); 2 ♂♂, 28 and 30.i.1948, Blundell's, A.C.T. (S. J. Paramonov); 1 ♂, 19.i.1935 (M. Fuller), Blundell's, A.C.T.; 1 ♂, 22.i.1935, Blundell's (W. Rafferty); 1 ♂, Jan. 1922, Blue Mountains (C. Deuquet); ♂♂, 2 ♀♀, 1.i.1938, Tindery, N.S.W. (Mackerras); 2 ♂♂, 22.xii.1937, Blundell's, A.C.T. (Mackerras); 1 ♂, 12.ii.1934, Coree Creek, A.C.T. (F. J. Gay); 1 ♀, 9.ii.1948, Bendora, A.C.T. (S. J. Paramonov); 3 ♀♀, 19.vii.1924, Stanthorpe, Queensland; 1 ♀, 22.xii.1922, Jannali, near Sydney (F. J. Gay).

44. Trichophthalma glauerti, sp. nov. ♂

This species belongs to the group of *T. harrisoni* Macker., but is readily distinguished by the absence of thin golden, depressed hairs on mesonotum and tergites; by the broader frontal stripe; by the extremely long hairs on eyes etc.; it is closely related to *T. fortei*, sp. nov.

Eyes separated by a narrow frontal stripe, which is a little broader than the anterior ocellus and a little shorter than the ocellar triangle. There is a distinct keel at the top of the frontal triangle, the sides of which have 2 tufts of yellowish erect hairs, whereas the middle and lower parts are bare. Ground colour of frons dark, that of the face yellow. Face with very long yellowish hairs on the sides, with the median part bare. No furrow between the face and the eyes. Ground colour of the basal joints of antennae yellow, that of the 3rd dark. First antennal joint distinctly longer than the rounded 2nd one. The

basal part of the 3rd joint is shorter than the 2 basal joints together, which are yellowish-haired; palpi yellow, with some similar hairs. Proboscis black, normal. Eyes very long, especially on the lower ½, haired.

Mesonotum without any traces of the dusted longitudinal stripes at sides (which are present in *T. harrisoni*) or similar submedian stripes. Hairs erect, very long and dense, yellow, on the under side of thorax a little lighter. Similar hairs are present on the scutellum; no golden depressed hairs on mesonotum and no long black hairs on scutellum as in *T. harrisoni.*

Wings hyaline, a little yellowish along the costa. Halteres yellow; legs yellow. Alula triangular; at base acute.

Abdomen in colour very similar to that of *T. harrisoni,* but the dark median stripe and the dark margins of tergites are not so dark and not so extensive. Golden depressed hairs and black erect hairs absent.

All hairs on abdomen are yellow, only apical part of some a little darker. The 3 genital plates at base of nearly equal width; the middle plate is at base broad, but triangular, regularly tapering towards the apex.

This species is a little stouter than *T. harrisoni* Macker.

Length of body 10 mm., of wing 9.5 mm.

5 ♂♂, Yallingup, W.A. (Western Australian Museum). Type in the Western Australian Museum; cotype in Division of Entomology Museum, C.S.I.R.O., Canberra.

45. Trichophthalma fortei, sp. nov. ♂

Closely related to *T. glauerti,* sp. nov., but differs in the following characters:

(1) Wings along the costa narrowly but intensely dark brown, the boundary of this coloured area being rather sharp;

(2) Mesonotum with 2 very broad submedian grey stripes, which are not very clearly defined, though always distinguishable;

(3) Basal 2 joints of antennae of nearly equal length, as long as broad, 3rd joint longer than both basal joints together;

(4) The sides of abdomen not yellow as in *T. glauerti,* but reddish, and the greyish colour along the dark median stripe is a little darker and more extensive;

(5) Hairs on the eyes, on the ocellar triangle, and on the mesonotum shorter than in *T. glauerti;*

(6) There is a more marked contrast between the colour of upper and under side of the thorax than in *T. glauerti*; in *T. fortei* the upper side is yellow-haired, and under side white-haired, whereas in *T. glauerti* both upper and under sides are yellowish-haired, the colour of the upper side being slightly more intense.

Length of body about 10 mm.

1 ♂, 2.i.1941, Capel, W.A. (P. N. Forte), type in Western Australian Department of Agriculture; 1 ♂, same locality and data, but smaller and has on both wings a supernumerary veinlet, connecting the vein r_{2+3} and the base of r_4;

2 ♂ ♂, Jan. 1935, Nornalup, W.A. (P. N. Forte) (one of these in the Division of Entomology Museum, C.S.I.R.O., Canberra.

TABLE 1

A COMPARATIVE LIST OF AUSTRALIAN TRICHOPHTHALMA SPECIES SEPARATED INTO GROUPS

Mackerras 1925	*Paramonov* 1953	*Mackerras* 1925	*Paramonov* 1953
rosea Macq.	1. rosea Macq.	punctata Macq.	28. punctata Macq.
eques Schiin.	=2. bivittata Westw.	punctata orientalis Macker. var. minima Macker.	
	2*a*. forma *coerulea* nov. ♂, ♀		
	2*b*. bivittata wheeleri Beq.		
	3. *alulata*, sp. nov.		=29. orientalis Macker.
laetilinea Walk.	4. laetilinea Walk.	fulva Walk.	30. fulva Walk.
ricardoae Lichtw.	5. ricardoae Lichtw.		31. *lutea*, sp. nov. ♂
albimacula Walk.	6. albimacula Walk.		
	6*a*. *occidentalis*, subsp. nov.	leucophaea Walk.	32. leucophaea Walk.
	7. *waterhousei*, sp. nov. ♂, ♀	longirostris Macker.	
	8. *thomsoni*, sp. nov. ♂		=33. degener Walk.
variolosa Lichtw.	9. variolosa Lichtw.		34. *regina*, sp. nov. ♂
grisea Macker.	10. grisea Macker.		35. *griseola*, sp. nov. ♂
primitiva Walk.	11. primitiva Walk.		
		confusa Macker.	36. confusa Macker.
nigripes Macq.	=12. scapularis Big.	nicholsoni Macker.	37. nicholsoni Macker.
	12*a*. var. *pallipes* var. nov.	dubiosa Macker.	38. dubiosa Macker.
nigrovittata Macker.	13. nigrovittata Macker.	bivitta Walk.	39. bivitta Walk.
bancrofti Macker.	14. bancrofti Macker.	bivitta nigricosta Macker.	39*a*. bivitta nigricosta Macker.
	15. *froggatti*, sp. nov. ♂		
	16. *doddi*, sp. nov. ♂, ♀	trilinealis Macker.	40. trilinealis Macker.
novae-hollandiae Macq.	17. novachollandiae Macq.	ruficosta Macker.	41. ruficosta Macker.
		griseolineata Macker.	42. griseolineata Macker.
obscura Westw.	18. *fullerae*, nom. nov.		
	19. *mackerrasi*, sp. nov. ♂	harrisoni Macker.	43. harrisoni Macker.
fusca Macker.	20. fusca Macker.		44. *glauerti*, sp. nov. ♂
	21. *calabyi*, sp. nov. ♂		45. *fortei*, sp. nov. ♂
intermedia Macker.	22. intermedia Macker.		
costalis costalis Macker.	23. costalis costalis Westw.		
	23*a*. *costalis soror*, subsp. nov.		
costalis apicalis Macker.	24. apicalis Macker.		
rufonigra Macker.	25. rufonigra Macker.		
subcostalis Macker.	26. subcostalis Macker.		
	27. *transversa*, sp. nov. ♂		

Note.—Among the material examined from Western Australia there are specimens which differ from *T. fortei* by the very slightly darkened costal area of wing etc., but these specimens are in too poor a condition to allow a satisfactory determination.

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List of Species